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Influence of Plants other than the Food Plants of their Host on Host-Finding by Tachinid Parasites

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Earlier work indicated that food plants of the tenthredinid sawflies attacked by *Drino bohemica* Mesn. and *Bessa harveyi* Tns. influence host-finding by these tachinid parasites (Monteith, 1955, 1958a). There is a high degree of interaction between stimuli produced by the host larvae and by their food plants (Monteith, 1955, 1958b).

It was observed during field studies that the percentage parasitism by *B. harveyi* of the larch sawfly, *Pristiphora erichsonii* (Htg.), varied with increasing height above the ground and in different sections of tamarack trees, *Larix laricina* (DuRoi) K. Koch, on which the sawfly larvae were feeding. It appeared that shrubs and trees other than *L. laricina* influenced host-finding by *B. harveyi*.

This is a report on results of an investigation into the influence of plants other than the food plants of their host on host-finding by *B. harveyi* and *D. bohemica*. Sufficient data on the influence of meteorological factors were obtained to show that such factors probably were not responsible for the effects attributed to the non-food plants.

There are many references on the activities of insects at different heights around trees and other plants but most of these were on non-entomophagous species and involved the use of bait traps (Bellamy and Reeves, 1952) or light traps (Herms, 1947; Ficht and Hienton, 1941; and Frost, 1958).

There are few references to the activities of entomophagous insects at different heights. McLeod (1951) found that the percentage parasitism of a lodgepole needle miner, *Recurvaria* sp., by four species of parasites was much higher from samples taken on branches more than 30 feet above the ground than from samples taken below this height. Parasitism of blowfly puparia by the chalcid *Nasonia vitripennis* (Walk.) was much higher in traps at ground level than in those 15 feet above the ground but parasitism by *Brachymeria fonscolombei* (Dufour) increased from that in the traps at ground level to those 15, 30 and 45 feet above the ground (Roberts, 1933). These authors did not determine the reasons for the differences in the percentage parasitism at different heights.

Material and Methods

Bessa harveyi was used for field studies because of its high population in the field. The line of *Drino bohemica* used in previous studies (Monteith, 1955, 1958a, and 1958b) was used for the laboratory phases of this work. These two species are sufficiently similar in their innate searching behaviour that data obtained with one is a measure of the responses by the other under similar conditions in their respective environments (Monteith, unpublished data).

I. *Parasitism in the field*

Field studies were on host-finding by *B. harveyi* of its preferred host *Pristiphora erichsonii*. They were conducted at sites in which *Larix laricina* was the most abundant tree but was mixed with *Picea glauca* (Moench) Voss and *P. mariana* (Mill) B.S.P., *Alnus rugosa* (DuRoi) Spreng var. *americana* (Regel)

Fern. and *Salix* species. In these sites the ground was moderately dry and was covered with *Ledum groenlandicum* Oeder, with some patches of grass. In 1953 observations were made in the vicinity of Gold Pines, in 1954 and 1955 at Longlac, both in northwestern Ontario.

Samples of larvae were taken from different sectors of *L. laricina* trees. The term "sector" represents a wedge-shaped section of varying width and three feet thick from any horizontal layer of a tree. The width of the outer edge of different sectors was set arbitrarily depending on the position of other trees. Sectors were sampled at different heights in trees. The number of larvae sampled in each sector was not in proportion to the sawfly population in each sector. It was necessary to do more searching for colonies feeding on *L. laricina* branches in contact with other species of trees or with the plants making up the ground cover than in sectors not touching other species because of the lower population in the former. Only where there was evidence that a colony was actively feeding were samples taken. This ensured that the larvae had not just crawled onto the branch or fallen from a higher one. It was necessary to catch larvae that fell from a colony being sampled because the mature larvae drop readily when disturbed.

Larvae were picked as randomly as possible from colonies, up to ten per colony. Many colonies had a smaller number. As first and second instar larvae are not parasitized they were not included in the samples. Only well-fed, apparently healthy colonies were sampled to avoid possible differences in the attractiveness of the larvae to *B. harveyi*.

B. harveyi deposits a macrotype egg that can be readily seen. The number of eggs on the larvae in the samples from comparable sectors were totalled. The total number of eggs, indicating the number of successful searches, was expressed as a percentage of the total number of larvae sampled in each sector. In the case of superparasitism, all the eggs were counted as each was indicative of a successful search.

A. *Parasitism at different heights.*—Trees were divided into levels depending on the height above the ground as follows: below three feet, three to six feet and above the ground cover, six to nine feet, 10 to 13 feet, and over 15 feet. The samples taken from the lowest level were either touching the foliage of or below the tips of the ground cover which was about three feet high. All other samples taken in this phase of the study were from branches of *L. laricina* not facing and not in close proximity to other trees. Samples taken in 1953 consisted of 378 larvae from 50 colonies, in 1954 of 936 larvae from 110 colonies.

B. *Parasitism in different sectors of food trees of host in relation to the position of other trees.*—*L. laricina* trees were divided into sectors on a basis of the position of other trees within two feet of that from which sawfly samples were taken. The sectors used in this phase of the study were: facing away from other trees, facing, and touching. The facing sectors were divided into facing *L. laricina*, *P. glauca*, and other species of trees. The touching sectors were similarly subdivided.

The "facing" sector included branches that were facing some other tree or shrub but with the tips of the branches, on which the larvae were feeding, not closer than six inches to or more than 24 inches from the other tree. The "touching" sector included that section of any *L. laricina* tree where the branches came in contact with those of another tree. No samples of larvae were taken from branches of *L. laricina* that overlapped other tree species sufficiently that the amount of foliage on the former was reduced.

The numbers of larvae sampled in this phase of the study were 1,343 in 1954 and 1,617 in 1955. All were taken from branches in the three to six and six to nine foot levels above the ground.

C. *Light intensity, temperature and wind velocity.*—These factors vary continuously under field conditions. Measurements were made as each sample of larvae was taken in 1955, to show whether these factors might be responsible for the difference in percentage parasitism in different sectors of *L. laricina* trees.

Samples were selected to provide data on the number of eggs laid on larvae at different light intensities with the temperature and wind velocity constant. Others were selected to provide a series of readings at different temperatures and wind velocities. It was extremely difficult to obtain series of samples because of the many combinations possible and the continual changes. During the days in which samples were taken, the light intensity reflected from the larval feeding sites varied from 150 to 1200 foot candles, the wind from zero to 600 feet per minute, and the temperature from 15° to 35°C.

A further check on the influence of these three factors on the incidence of parasitism was made by tabulating all samples for each tree sector in relation to light intensity and cloud cover without regard to temperature or wind velocity. Data were similarly tabulated on parasitism in each sector according to wind velocity and temperature.

The light intensity to which a colony of sawfly larvae would be exposed changes considerably during any day even if there is no change in the amount of cloud cover. To check the extent of such changes, light reading at four branches on each of four trees were taken at different times through the day under different conditions of cloud cover.

Light intensity in all cases was measured with a Weston Master II Universal Exposure Meter, which has a range of up to 1600 foot candles. Readings were taken of the light reflected at the feeding site from a 8″ x 8″ piece of light blue Bristol Board. Wind velocity was measured with a Bacharach Grill Velocity Finder, Model M.R.F. (Bacharach Industrial Instrument Co.). This model has a range from 0 to 1,000 feet per minute. The temperature was measured with a mercury thermometer.

II. *Laboratory Studies*

The influence of plants other than the food plant of the host on host-finding was studied in the laboratory using *D. bohemica* in two types of tests: one in an olfactometer, the other with trees in a cage.

A. *Olfactometer.*—The influence of odours from plants other than those consumed by the sawflies that are attacked by *D. bohemica* was tested in a Y-tube type olfactometer (Monteith, 1955, Fig. 2). The effect of these plants on olfactory responses by the parasites was examined in four series of tests as follows:

(1) The odour of *L. groenlandicum* was tested against odourless air to determine if the odour of the plant is attractive or repellent.

(2) The odour of *L. groenlandicum* was tested in two ways against that of *P. glauca* to determine the influence of the former on the parasite's response to the odour of the food plant of its host: a. Equal quantities of *P. glauca* foliage were placed in the air stream entering each side of the olfactometer. A piece of *L. groenlandicum* about the same size as the branch of *P. glauca* in either side was placed in the air stream entering one side of the olfactometer; b. *P. glauca* foliage as in "a" but with the piece of *L. groenlandicum* one-half the size of that used in "a".

(3) The odour of L. groenlandicum was tested with that of D. hercyniae larvae to determine the influence of the plant on the parasites' response to the odour of its host. An equal number of larva were placed in the air stream entering each side of the olfactometer and a piece of *L. groenlandicum* equal to that used in Series 2a added to one side. Each series of experiments consisted of 8 tests each using 20 flies. There were 10 tests in Series 3. Different groups of flies were used in successive tests.

(4) The odour of *P. glauca* foliage was tested against odourless air during another phase of the study (unpublished data) and is included here to show the influence of *L. groenlandicum*. A different group of 15 flies were used in each of eight tests.

B. *Parasitism in different sectors of food trees of host in relation to the position of other trees.*—Two trees each of *P. glauca* and *Pinus resinosa* Ait. were placed in a cage six feet square and 3½ feet high (Monteith, 1955, Fig. 3) so that the ends of the branches of each were in contact with those of the other three. The two *P. glauca* trees were beside each other and facing the two *P. resinosa*. Each tree was then considered to be divided into four vertical sections: touching peripheral, closest to the other species of tree, parallel to the latter, and including the outer half of the branches; touching inner, facing the other species of tree but the inner half of the branches; away inner, the inner half of branches that faced away from the other species of tree; and away peripheral, the outer half of the branches that faced away from the other trees.

Larvae were placed on their preferred food tree, twelve to a tree with three in each of the four sections. As the trees were about 3 feet high and their natural shape caused them to taper above the 1½ foot level, the larvae in each sector were kept below this level. They were tied in a given position (Monteith, 1955) to prevent them from moving from one section to another. Twelve parasites were used in each test. Eighty-one one-day tests (Monteith, 1955) were made using parasites from seven generations.

The trees used and the sawfly species on each were: *Picea glauca* with *Diprion hercyniae* (Htg.); and *Pinus resinosa* with *Neodiprion lecontei* (Fitch). The positions of the trees in the cage were changed after every third test by rotating them in a clock-wise direction keeping the orientation of the trees constant. Sufficient influorescent and incandescent lights were used to make the light intensity on all sides of the trees nearly equal.

Results

Influence of Non-food Plants in the Field

Height Above Ground

Parasitism of *Pristiphora erichsonii* by *Bessa harveyi* was very different at different heights in *Larix laricina* trees. The differences were highly significant in all three years ($P < .001$, Table I). The percentage parasitism of all larvae was lower in 1954 than in 1953 or 1955 but this did not change the pattern of parasitism at different heights.

Parasitism at the level of the ground cover was uniformly very low each year: 10, 11, and 13 per cent in 1953, 1954, and 1955 respectively. The percentage parasitism at all other heights was much higher, though above 15 feet it was not as high as at the intermediate levels. In 1954, parasitism at the six to nine foot level was over 10 per cent higher than at the three to six foot level. In 1953, it was only 2.5 per cent higher at the six to nine foot level than at the three to six foot level. In 1955 it was six per cent higher at the three to six

Table I

Percentage Parasitism in the Field by *Bessa harveyi* Tns. of *Pristiphora erichsonii* (Htg.) Feeding at Different Heights in *Larix laricina* (DuRoi) K. Koch not in Close Proximity to Other Species of Trees

Height above ground	1953		1954		1955	
	Number larvae sampled	% ** parasitized	Number larvae sampled	% ** parasitized	Number larvae sampled	% ** parasitized
Level of ground cover	96	10.4*	162	11.1*	38	13.2*
3′ – 6′	190	58.4	209	32.1	438	75 6
6′ – 9′	92	60.9	248	42.3	126	69.8
10′ – 13′			220	34.5		
Over 15′			97	19.6		

*X^2 between parasitism at different heights;
in 1953, 68.7; in 1954, 52.5; in 1955, 68.3 $P < .001$.
**The total number of parasite eggs expressed as a percentage of the number of host larvae collected.

foot level than at the six to nine foot level. There was apparently little difference in the searching pattern of the parasite at these two levels.

In 1954, when samples were taken at the 10 to 13 foot and over 15 foot levels, the percentage parasitism increased from the level of the ground cover up to the six to nine foot level and then decreased in the 10 to 13 foot level and again in the over 15 foot level.

Tree Sectors

The percentage parasitism by *B. harveyi* of *P. erichsonii* in different sectors of *L. laricina* trees varied in relation to the proximity of other species of trees and shrubs. Parasitism was much higher in 1955 than in 1954 and the differences in the percentage parasitism in the various sectors was more evident in 1955 though the differences between sectors in each year were highly significant ($P. < .001$, Table II).

In 1955, the percentage parasitism in the different sectors was: facing away from other trees, 74.3; facing *L. laricina*, 86.5; facing *P. glauca*, 39.4; facing other species of trees, 36.1; touching *L. laricina*, 75.9; touching *P. glauca*, 46.9; and touching other species of trees 35.9 (Table II). In those sectors where only *L. laricina* was present, parasitism ranged from 74 to 86 per cent whereas when other species of trees were present the parasitism was from 35 to 46 per cent. Parasitism in the facing *L. laricina* and touching *L. laricina* sectors was as high as in the facing away from other trees sector. Apparently it was not the presence but the species of the other tree close to the feeding site of the larvae that influenced host-finding by *B. harveyi*.

In 1954, the percentage parasitism in the different sectors was: facing away from other trees, 36.6; facing *P. glauca*, 35; facing other species of trees, 22.3; touching *P. glauca*, 28; touching other species of trees, 20.5 (Table II). With the exception of the parasitism in the facing spruce sector that in the facing away sector was higher than in those sectors where species of trees other than *L. laricina* were present.

Parasitism in the facing and the touching *P. glauca* sectors and the facing and the touching other species of trees sectors did not indicate definite differences

Table II

Percentage Parasitism in the Field by *Bessa harveyi* Tns. of *Pristiphora erichsonii* (Htg.) in Various Sectors of *Larix laricina* (DuRoi) K. Koch in Relation to Other Trees.

Sector of *L. laricina*	Other trees	1954		1955	
		Larvae sampled	% *** parasitized	Larvae sampled	% *** parasitized
Facing away+ from other trees	—	677	36.6*	564	74.3**
Facing other trees	*L. laricina*	—	—	37	86.5
	P. glauca	220	35.0	99	39.4
	Other species	103	22.3	144	36.1
Touching other trees	*L. laricina*	—	—	344	75.9
	P. glauca	226	28.0	215	46.9
	Other species	117	20.5	212	35.9

*X^2 between sectors = 19.9 $P < .001$.
**X^2 between sectors = 214.7 $P < .001$.
+1953 – facing away, 282 larvae sampled, 62.8% parasitized.
***The total number of parasite eggs expressed as a percentage of the number of host larvae collected.

in the percentage parasitism between the facing and the touching sectors. In 1954, the parasitism in the facing and touching *P. glauca* sectors was 35.0 and 28.0 respectively, whereas that for the facing and touching other tree species sectors was 22.3 and 20.5 per cent (Table II). In both cases the parasitism in the facing sector was higher than in the touching sector though the differences were small. In 1955, the parasitism in the facing and the touching other species of trees sectors were nearly the same whereas that for the touching *P. glauca* sector was higher than that in the facing *P. glauca* sector, 46.9 and 39.4 per cent respectively.

Influence of Microclimate

Light intensity was an exceedingly variable factor under field conditions. Measurements of the light intensity at four sites on each of four trees showed that on sunny days it varied continually from 100 to 600 foot candles. In as little as 20 minutes the intensity at a given site would change by more than 300 foot candles. As the eggs recorded from any sample may have been deposited during a period in which the light intensity varied considerably, and the light at sample sites in all sectors varied in this fashion, the differences in the percentage parasitism of *P. erichsonii* in different sectors of *L. laricina* apparently were not caused by differences in light intensity. When samples from different sectors were arranged on a basis of the light intensity at the branch from which each sample was taken there was no relationship between percentage parasitism and light intensity.

There was little, if any, difference at a particular time between the temperatures in different sectors of any *L. laricina* tree or clump of trees. Moreover, samples taken from different sectors at a constant temperature showed differences in parasitism similar to those in Tables I and II. Samples taken from similar sectors but at different temperatures did not show any relationship between temperature and the pattern of parasitism. Thus, the temperature apparently did not cause the differences in percentage parasitism in different sectors.

Table III

Influence of the Odour of *Ledum groenlandicum* Oeder on Responses by *Drino bohemica* Mesn. to the Odour of its Host *Diprion hercyniae* (Htg.) and of *Picea glauca* (Moench) Voss, the Food Tree of its Host in an Olfactometer

Test Odour		Total number flies responded in 8 tests	Percent response to A	P
A	B			
L. groenlandicum	vs. odourless air	126	50.6	> .4
P. glauca	vs. odourless air	92*	75.0	< .001
P. glauca	vs. *P. Plauca* + *L. groenlandicum* (1:1)	139	52.5	> .1
P. glauca	vs. *P. glauca* + *L. groenlandicum* (1:1/2)	125	65.6	< .001
Larvae	vs. larvae + *L. groenlandicum*	185+	57.3	> .04

Larvae vs. odourless air. 80.9% to the larvae (Monteith, 1955).
*15 flies per test, 20 flies in the others.
+10 tests.

There was apparently no relationship between the wind velocity, within the range when work in the field could be conducted, and the percentage parasitism of the sawfly samples from any particular sector. When samples from different sectors were arranged on a basis of the wind velocity at the branch from which each sample was taken, those from different sectors at a constant wind velocity showed differences in parasitism similar to those in Tables I and II. Samples from similar sectors but at different wind velocities did not show any relationship between wind velocity and the percentage parasitism.

Influence of Non-food Plants in the Laboratory

Olfactory

Olfactometer tests indicated that the odour of *L. groenlandicum* has an influence on the searching behaviour of *Drino bohemica* when tested in the olfactometer. When the odour of this shrub was tested against a current of odourless air, there was no significant difference ($P > .4$) in the number of flies entering either arm of the Y-tube (Table III). The odour of this plant was neither an attractant nor a repellent. This agrees with field observations where the flies frequently rest on *L. groenlandicum* bushes but return to sectors of the *L. laricina* above the ground cover during their search for sawfly larvae.

When the odour of *P. glauca* was tested against odourless air the response to the arm with the odour was 75 per cent (Table III). The odour of the tree was highly attractive. When the odour of *P. glauca* was passed through both arms with a branch of *L. groenlandicum*, equal in bulk to that of the *P. glauca*, in one side, the response to the arm with only the odour of *P. glauca* was 52.5 per cent. This difference was not significant ($P > .1$). When the amount of *L. groenlandicum* in the one arm was reduced by half, the response to the arm with only the odour of *P. glauca* increased to 65.5 per cent and the difference was significant ($P < .001$, Table III). In this case, the response was not as high as that to the odour of *P. glauca* when tested against odourless air and indicated a degree of masking of the odour of *P. glauca*. In the test with the larger

Table IV

Parasitism by *Drino bohemica* Mesn. of *Diprion hercyniae* (Htg.) Larvae in Different Sectors of *Picea glauca* (Moench) Voss and of *Neodiprion lecontei* (Fitch) in *Pinus resinosa* Ait. in the Laboratory

Sectors of trees	Number of eggs laid on 399 larvae exposed in each tree sector	
	D. hercyniae on *P. glauca*	*N. lecontei* on *P. resinosa*
Touching peripheral	261*	128**
Touching inner	372	165
Away inner	375	157
Away peripheral	362	168

*X^2 (between number of eggs in each sector of *P. glauca* = 184.97 $P < .001$
** X^2 (between number of eggs in each sector of *P. resinosa* = 6.43 $P > .07$

amount of *L. groenlandicum*, the odour of *P. glauca* from both arms evidently was masked.

The response to the odour of *D. hercyniae* larvae tested against odourless air was 80.9 per cent (Monteith, 1955). In the current study, when the odour of *D. hercyniae* was passed through both arms of the olfactometer with the odour of *L. groenlandicum* (half-sized branch) in one side, the response to the arm without the odour of the shrub was 57.3 per cent, the difference between the number of parasites that entered each arm was barely significant ($P > .04$). If the odour of *L. groenlandicum* had no effect the distribution of parasites would have been 50 per cent to each arm. If only the odour of the larvae in the arm with the shrub was masked, then the response to the other arm would have been much higher (as in the case with odourless air). The response obtained indicated a degree of masking of the larval odours from both arms.

Parasitism in Different Sectors of Food Trees of Host in Relation to Other Trees

The odours of the trees enclosed in the tree cage influenced host-finding by *D. bohemica*. The number of successful searches by *D. bohemica* for *D. hercyniae* on *P. glauca* was much lower in the touching peripheral section, 261, than in the touching inner, the away inner, and the away peripheral sections, where the number of eggs were 372, 375, and 362 respectively. The differences were significant (Table IV). The odours of the *P. resinosa* in contact with the *P. glauca* apparently caused the parasites to search more frequently in the sections of the *P. glauca* not in contact with the *P. resinosa*. There was no significant difference between parasitism in the touching inner, the away inner, and the away peripheral sections (Table IV).

The number of successful searches for larvae of *N. lecontei* on red pine was also lower in the facing peripheral section, 128, than in the touching inner, the away inner, and the away peripheral sections, where they were 165, 168, and 157 respectively (Table IV), but the differences were not significant at the five per cent level.

Discussion

The influence of plants other than the food plants of the host on host-finding by tachinid parasites was evident both in the field and in the laboratory. The very low percentage parasitism by *Bessa harveyi* of *Pristiphora erichsonii* larvae feeding at or below the top level of the plants that comprised the ground cover was apparent in random samples taken during studies on other aspects of

host-parasite relationships. When this was investigated further, the differences in parasitism at different heights was quite striking. The parasitism at the level of the ground cover was only 10 to 13 per cent during three consecutive years whereas that in the three to six foot and the six to nine foot levels ranged from 32 to 75 per cent. These differences indicated a strong effect by *Ledum groenlandicum* and other plants in the ground cover on host-finding by *B. harveyi.*

The flight behaviour of *B. harveyi* in the field showed that the odour of *L. groenlandicum* was not repellent because the parasites frequently rested on it and some larvae were parasitized while feeding on branches in contact with this plant. The fact that *Drino bohemica* entered the arm of the olfactometer with the odour of *L. groenlandicum* in the same numbers as the arm with odourless air also indicated that the odour of this plant was neither attractive nor repellent. Tests in the olfactometer indicated that the odour of *L. groenlandicum* tended to mask that of the host and the food plant of the host. Since both these odours assist tachinid parasites to find their host (Monteith, 1955), the masking effect could be very important.

Differences in parasitism in different sectors of *L. laricina* trees in relation to other trees were similar to those at different heights but not so striking (Table II). The percentage parasitism of larvae in different sectors of trees in the laboratory (Table IV) showed that these differences were caused by the odour of other trees. There was no such effect when two or more *L. laricina* trees were in contact as shown by the fact that the percentage parasitism of larvae in the facing and the touching *L. laricina* sectors was as high as that in the facing away sectors (Table II). This was true even in those touching *L. laricina* sectors where the light intensity was very low.

Differences in the percentage parasitism in the four sections of *P. glauca* trees in the laboratory (Table IV) were similar to those in different sectors of *L. laricina* trees under field *conditions* (Table II). The number of successful searches by *D. bohemica* for *D. hercyniae* in the touching peripheral sector was significantly lower than those in the touching inner, away inner, and away peripheral sections (Table IV). There was no significant difference between the number of successful searches in the other three sections. Thus the *P. resinosa* influenced host-finding in the touching peripheral section of the *P. glauca* trees, the masking effect was only evident where the branches of the two species of trees came into contact.

There were no significant differences between the parasitism of *N. lecontei* in the four sections of the *P. resinosa* trees (Table IV). Host-finding in the *P. glauca* trees, the food plant of the preferred host of *D. bohemica*, was influenced by the odour of the less attractive *P. resinosa* but searching in the latter was not influenced to a significant degree by the odour of the *P. glauca.* The conclusion that the difference in parasitism in the facing peripheral section of the *P. glauca* was largely due to the masking effect is supported by various facts. The light intensity was nearly equal on all sides of the trees and the positions of the trees were rotated so that neither light intensity or positional effects were responsible. The host larvae were exposed in the lower 1½ feet of the trees so that height in the cage was not important. Shading was not important because there was no significant difference in the number of successful searches between the touching inner, the away inner, and the away peripheral sections of the *P. glauca*, or between the four sections of the *P. resinosa* trees in the laboratory. In the field, parasitism in the centre of a clump of *L. laricina* was sometimes as high as in the peripheral areas, though the light intensity was comparatively low in the centre.

A further indication that the effect was due to the masking of one odour with another is that the odour of each of the sawfly species and that of their preferred food trees were highly attractive to *D. bohemica* when tested against odourless air or a pine-needle oil standard (Monteith, 1955).

In the field the degree of masking by the odour of *L. groenlandicum* and other plants making up the ground cover appeared to be greater than that by *P. glauca* and other species of trees. The effect of the odour of species of *Alnus* and *Salix* apparently was greater than that of *P. glauca*.

Other species of trees, shrubs, and grasses in close proximity to the branches of *L. laricina* on which *P. erichsonii* larvae were feeding had a definite effect on the searching behaviour of *B. harveyi* because of the masking of the odours of the larvae and their food tree. This provided a degree of protection for larvae feeding on branches of *L. laricina* in close proximity to other plants, especially those in contact with the ground cover where only 10 to 13 per cent were parasitized compared with as much as 86 per cent in sectors where only *L. laricina* was present. The proportion of the sawfly population that escaped parasitism could be important to maintenance of the population, especially in years when apparent parasitism in unprotected sectors is high. The number of sawflies feeding on branches of *L. laricina* in contact with other species of plants was generally lower than that on branches not in contact with other species. Though the amount of foliage on branches touching other species might be reduced, the larvae had sufficient foliage for development compared with larvae on heavily infested branches. These larvae had the double advantage of having sufficient food and a degree of protection from the parasite.

The protective nature of plants other than the food plant of the host was shown by Richards (1940) who found that *Apanteles rubecula* Marsh did not attack larvae of *Pieris rapae* (L.) on cabbage plants placed among grass or flower beds whereas 50 per cent of the larvae on control plants among other cabbages were attacked. He believed the difference was due to the attractiveness of large plots of cabbages. In addition to this effect it is quite likely that the odours of grass, flowers, and shrubs masked that of the cabbage plants in close proximity to them and of the larvae on these cabbage plants.

The protection afforded a plant by those in contact with it was shown by MacAloney (1932). He found that white pine trees, *Pinus strobus* L., were relatively immune from attacks by the white pine weevil, *Pissodes strobi* (Peck) until their leaders grew through the crown canopy of the other species. One reason for this may have been the masking of the odour of *P. strobus* by the plants in close proximity to them.

Climatic Factors

The variation in light intensity and cloud cover, the small differences in temperature in different sectors of the trees, the lack of influence by the wind, and the high percentage parasitism of larvae when only *L. laricina* were present regardless of the climatic factors, indicated that they were not the major factors influencing the differences in parasitism in different sectors of the trees.

The results obtained in the laboratory under controlled conditions of light, temperature, humidity and air movement indicate that the odours of the other plants were primarily responsible for these differences. Temperatures in the range that occurred during the period of study (16° - 32°C.) appeared to have little effect on the behaviour of *B. harveyi*. This parasite was observed in the stands of *L. laricina* on all days when samples were taken. Similar observations were made on *Exeristes roborator* (F.) by Baker and Jones (1934) who found

that only extremes of temperature, that is below 10° and above 32°C., tended to restrict the activity of adults of this parasite.

Similarly it is unlikely that the temperatures recorded influenced the feeding activity of the larch sawfly. Green and deFreitas (1955) found that wind, relative humidity and light seemed to have little effect on the feeding activity of two other species of sawflies, *Neodiprion lecontei* and *N. americanus banksianae* (Roh.). Temperature affected the rate of frass drop more than did other meteorological factors. However, temperatures above the maximum for frass drop were seldom encountered in the field.

In addition to the fact that temperatures in different sectors of *L. laricina* trees at a particular site varied very little, the parasite eggs counted in any sample were deposited over a period of time previous to sampling. During this time the temperatures may have changed in both sectors being compared. This further reduced the importance of temperature as a factor influencing the differences in parasitism in different sectors.

It is apparent that the differences in the percentage parasitism by *B. harveyi* of *P. erichsonii* in different sections of its food tree was primarily due to the masking effect of the odours of plants other than the food tree. Although climatic factors may influence parasite behaviour they were not responsible for the differences in parasitism in different sectors of the same trees. This conclusion is supported by results obtained in the laboratory under controlled conditions.

Summary

Host-finding by tachinid parasites is influenced by plants other than those fed on by the tenthredinid sawflies that they attack. In the field, the percentage of larvae of the larch sawfly, *Pristiphora erichsonii* (Htg.), attacked by *Bessa harveyi* Tns. varies with their positions on *Larix laricina* (DuRoi) K. Koch trees relative to the positions of other plants. Host-finding by *B. harveyi* is influenced by the presence of shrubs beneath the *L. laricina* trees and by the close proximity of *Picea glauca* (Moench) Voss or other species of trees. The effect was not caused by temperature, light intensity or air velocity. In the laboratory, tests with *Drino bohemica* Mesn. of olfactory stimuli from food plants and non-food plants showed that the latter tend to mask the odours of host larvae and of their food plants. The masking effect could be of importance in aiding a larger proportion of the sawfly population to survive.

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Note on Parasitism of Two Coccinellids, *Coccinella trifasciata perplexa* Muls. and *Coleomegilla maculata lengi* Timb. (Coleoptera : Coccinellidae) in Ontario

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In the Belleville, Ontario, district parasitism of 646 adults of *Coccinella trifasciata perplexa* Muls. by *Perilitus coccinellae* (Schrank) (Hymenoptera: Braconidae) was approximately seven per cent and of 363 adults of *Coleomegilla maculata lengi* Timb. 16 per cent in 1959. Mature parasite larvae emerged from both species of host adults after 20.9 ± 6.2 days of host feeding in the laboratory. The duration of the pupal stage was 10.7 ± 0.4 days and of the adult stage 8.9 ± 5.2 days (22°C. and 65 per cent R.H.). The host beetle usually remained inactive after the emergence of the parasite. Its feet were often entangled in the silk of the parasite's cocoon, and it died within 10 days. *P. coccinellae* emerged from adults of *C. maculata* obtained from fourth-instar larvae collected in the field and reared to the adult stage in the laboratory, and also from pupae collected in the field. This is the first authenticated record of this parasite attacking a host stage other than the adult in the field (Clausen 1940), and the second record for this species in Canada (Hudon 1959). Parasitized females of *C. maculata* laid fertile eggs up to 10 days before the emergence of *P. coccinellae.*

Total parasitism of both *C. trifasciata* and *C. maculata* by *Hyalomyodes triangulifera* (Loew.) (Diptera: Tachinidae) and an unidentified nematode was under one per cent. Thompson (1954) listed *C. maculata,* but not *C. trifasciata* as a recorded host for *H. triangulifera.*

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Parasites of *Neodiprion pratti banksianae* Rohwer in Northern Ontario[1]

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Introduction

Outbreaks of the jack-pine sawfly, *Neodiprion pratti banksianae* Rohwer, occur in northern Ontario at irregular intervals. Two independent outbreaks within 50 miles of each other – one on Great Cloche Island (McGugan *et al.*, 1952) which lies in the North Channel of Lake Huron between Manitoulin Island and the mainland, and the other near Nairn Centre, approximately 30 miles west of Sudbury, Ontario – offered an opportunity to study the parasitism of this important defoliator. In 1954, when the study was started, heavy defoliation had been reported for several years in the Great Cloche outbreak, and light defoliation had occurred for one year in the Nairn Centre outbreak. Populations decreased in the Great Cloche area but remained relatively constant at a low level in the Nairn Centre area during 1955 and 1956, when the work was completed.

The principal host of this sawfly, and the only one on which it was found in the present study, is jack pine, *Pinus banksiana* Lamb. Other host trees on which this species has been reported feeding, are Scots pine, *P. sylvestris* L., and red pine, *P. resinosa* Ait. (Atwood and Peck, 1943).

Briefly, the seasonal history of *N. p. banksianae* is as follows: it overwinters in the egg stage, eclosion occurring in late May. The larvae, which feed primarily on old foliage, are not fully developed till mid-July. They then spin cocoons in the duff or on the lower ground cover, from which adults emerge during September. Females lay their eggs in the current year's needles. According to Atwood and Peck (1943) the full egg complement of one female is usually laid on one twig.

Results

Parasitism of each of the three immature phases of the sawfly's life history—the egg, feeding stage larva and cocooned larva—was studied. In the lists of parasite species that follow, a simple system has been used to include information on the life histories of the parasites. It is usual to designate a parasite which attacks, say, the larva as a larval parasite, but such a designation does not distinguish between larval parasites that emerge as adults from the host larva and those that emerge from later host stages. The system used in the following lists permits such information to be easily and succinctly presented. In it the various stages in which a host may be attacked or from which the parasite may emerge are represented by lower-case letters, "e" for egg, "l" for larva, "pp" for prepupa, "p" for pupa, and "a" for adult. These symbols are placed in a simple two-letter formula, in which the first letter indicates the host stage attacked and the second the host stage from which the parasite emerged, the two symbols being separated by a colon. Thus the formula "e:l" summarizes the life history of a parasite that attacks the egg and emerges from the larva. Refinements to this simple system may be readily made. For instance, the active, free-living prepupal phase of certain sawflies and the inactive prepupal phase within the cocoon may be separated by use of the symbols "fpp" and "cpp." Further, if the exact larval instars involved are known, they may be included as subscripts, as "l_1:l_V." Finally, allowance may be made for cases in which exact information is lacking.

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If it is unknown whether the parasite emerges from the prepupa or pupa, the letter "c" may be used to denote "cocoon." When no information is available, a question mark may be substituted for a letter, as "?:p," indicating a parasite which was obtained from a host pupa with no further knowledge of its life history available.

In the lists that follow, the appropriate formula summarizing life history information is placed in brackets following the scientific name and authority of each parasite species. It is suggested that this system might be generally adopted in listings of parasite species by host insect species – it is usually prohibitively complex to subdivide such lists into the many possible combinations of host stages involved in the attack and emergence of parasites, and thus too often much valuable information is omitted.

Parasites of the egg

Approximately 30 egg clusters from each of the outbreaks were examined each year. There was no parasitism of this stage in the Great Cloche Island outbreak in any of the three years, nor at Nairn Centre in 1956. However, in 1954 and 1955, 3.8 and 1.3 per cent, respectively, of the eggs examined at Nairn Centre showed evidence of parasitism, either in the form of oval emergence holes approximately one-seventh the length of the egg slit, or of immature hymenopterous parasites within the host egg, discovered on dissection of the egg. The species responsible for the emergence holes could not be determined, and only one of the immature hymenopterous parasites, which were reared in vials after their removal from the egg, developed to an adult. It was identified as the encyrtid *Microterys fuscicornis* (How.) (e:e). The only previously recorded host of this species is the pine tortoise scale *Toumeyella numismaticum* (P. & McD.) (Peck, 1951).

Parasites of feeding stage larvae

In 1954, larvae were collected every two days at Nairn Centre and weekly at Cloche Island, and reared, some individually and some in groups. In 1955 and 1956 only two larval collections were made, and group rearings only were carried on. The following species were obtained from these rearings during the three years:

Diptera
- Tachinidae
  - *Diplostichus hamatus* (A. and W.) ($1_{III\&IV}$:c)
  - *Spathimeigenia spinigera* Tns. ($1_{III\&IV}$:c)

Hymenoptera
- Eulophidae
  - *Tetrastichus* sp. (1:c)
- Ichneumonidae
  - *Exenterus canadensis* Prov. ($1_{IV\&V}$:c)
  - *Exenterus platypes* Cush. (1:c)
  - *Euceros frigidus* Cress. (1_{I}:c)
  - *Horogenes* sp. (1:c)
  - *Lamachus tsugae* Cush. (1_{I}:c)
  - *Lamachus* sp. nr. *tsugae* Cush. (1_{I}:c)
  - *Lamachus* sp. nr. *contortionis* Davis ($1_{I\&II}$:c)
  - *Mesochorus* sp. ($1_{III\&IV}$:c)

TABLE I

PARASITISM IN LARVAL REARINGS

Year	Nairn Centre		Great Cloche	
	Number of larvae reared	Per cent parasitised	Number of larvae reared	Per cent parasitised
1954	1436	28.9	752	13.0
1955	305	20.3	364	16.2
1956	596	9.1	551	20.9

All the species obtained, with the exception of *Mesochorus* sp., *Tetrastichus* sp. and *Horogenes* sp., have been recorded from *N. p. banksianae* previously by Raizenne (1957) or Townes and Townes (1951). Species of *Mesochorus* and *Tetrastichus* have been obtained from other diprionids (Daviault, 1951; Townes and Townes, 1951), but no previous record of the genus *Horogenes* from diprionids has been found.

From the 1954 rearings only it was possible to determine the earliest host stage atacked by the parasites obtained in that year, and this information is given in the formulae following the scientific names above. Unfortunately, *Tetrastichus* sp. and *E. platypes* were not obtained in 1954 and this information is thus not available for these species. It is likely that the development of the host is in all cases arrested by the growth of the parasite before the cocooned host actually pupates, but since this is not definitely known the host stage from which adult parasite emergence occurs is shown simply as the cocoon.

All the Hymenoptera remained within the host cocoon throughout the winter, emerging as adults in the spring following attack. A variable percentage of the Diptera – ranging from 40 to 100 – emerged in the fall of attack; the remainder overwintered in the host cocoon and emerged the following spring. Overwintering of the Diptera did not appear to be related to time of attack or stage of the host attacked.

The proportion of parasitized larvae obtained from collections and subsequent rearings increased from 13 per cent to 21 per cent at Great Cloche during the three years studied, and decreased from 29 to nine per cent at Nairn Centre during the same period (Table I). The ichneumonids accounted for 80 per cent or more of the total parasitism, except at Nairn Centre in 1955 when they were largely replaced by the two tachinids as the most prominent elements in the complex (Table II). Table II also illustrates differences in relative abundance of individual species from year to year, in the two localities.

Parasites of the cocooned larva

It was only possible to study parasites that attacked the cocooned larva in the Great Cloche Island outbreak, because populations at Nairn Centre were too low to permit meaningful samples to be taken. At Great Cloche Island, the populations of cocooned larvae were sampled by taking 200 one-square foot quadrates beneath the crowns of infested jack pine trees in late August of 1954 and 1955. While taking these samples in 1954, it was found that a small proportion of larvae had spun their cocoons in the ground-cover foliage; therefore the ground-cover foliage on five one-hundred-square-yard areas was also

TABLE II

RELATIVE ABUNDANCE OF LARVAL PARASITES
expressed as per cent of total parasite emergence

Species	Nairn Centre			Great Cloche		
	1954	1955	1956	1954	1935	1956
Diplostichus hamatus	5.0	65.7	4.1	0	15.4	4.3
Spathimeigenia spinigera	6.2	17.1	4.2	20.0	0	2.1
Tetrastichus sp.	0	0	0	0	3.8	0
Exenterus canadensis	13.0	0	0	9.1	3.8	0
Exenterus platypes	0	0	0	0	0	4.3
Euceros frigidus	35.4	0	29.2	16.4	3.8	23.4
Horogenes sp.	0.6	0	0	0	0	0
Lamachus tsugae	19.3	0	12.5	43.6	0	40.4
Lamachus sp. nr. *tsugae*	0	2.9	0	0	23.2	0
Lamachus sp. nr. *contortionis*	18.0	14.3	50.0	7.3	46.2	25.5
Mesochorus sp.	2.5	0	0	3.6	3.8	0

searched for cocoons. Data from the latter were later converted to a square-foot basis for ease of comparison with soil samples. No cocoons were found in the ground-cover foliage while the 1955 soil sample was being taken, so the foliage sample was not repeated in that year.

Populations of sound cocoons (i.e., those containing healthy or parasitized prepupae) found in all samples were low. In 1954 there were 1.4 sound cocoons per square foot in the soil samples, with an additional 0.03 per square foot in the ground-cover foliage samples. In 1955 the population (soil samples only) was 1.2 per square foot. Parasitized prepupae averaged 0.5 per square foot in the soil and 0.01 per square foot in the foliage in 1954, and 0.4 per square foot in the soil in 1955 (Table III).

Rearing of cocoon samples resulted in recovery of parasite species that attacked the cocooned larva directly as well as those that attacked the larval stages, since all the latter were found to emerge as adults from the host cocoon. When the latter species were separated from the recoveries, the following seven remained as species that apparently attacked the cocooned larva directly:

Hymenoptera
- Eupelmidae
  - *Eupelmella vesicularis* (Retz.) (cpp:c)
- Pteromalidae
  - *Amblymerus verditer* (Nort.) (cpp:c)
  - *Habrocytus* sp. (?) (cpp:c)
- Ichneumonidae
  - *Agrothereutes lophyri* (Nort.) (cpp:c)
  - *Aptesis indistincta* (Prov.) (cpp:c)
  - *Delomerista diprionis* Cush. (cpp:c)
  - *Endasys subclavatus* (Say) (cpp:c)

TABLE III

ABUNDANCE OF COCOON PARASITES
Great Cloche Island

Species	Number of Parasites per sq. ft.	Per cent of Sound Cocoons Parasitised
	1954	
RECOVERED FROM COCOONS ON FOLIAGE		
Delomerista diprionis	.0059	19.7
Amblymerus verditer	.0030	10.0
Eupelmella vesicularis	.0007	2.3
Habrocytus (?)	.0004	1.3
	.0100	33.3
RECOVERED FROM COCOONS IN SOIL		
Delomerista diprionis	.34	24.3
Agrothereutes lophyri	.08	5.7
Aptesis indistincta	.08	5.7
	.50	35.7
Total parasitism (soil +foliage samples)	.51	35.7
	1955	
RECOVERED FROM COCOONS IN SOIL		
Endasys subclavatus	.40	38.3

All these species, with the exception of the doubtful *Habrocytus* sp., have been previously recorded from species of *Neodiprion* (Townes and Townes, 1951). *E. vesicularis* has also been listed as a hyperparasite of various species by Peck (1951); it is not known whether this species was acting in a primary or secondary capacity on *N. p. banksianae.*

In 1954, it was found that certain species – *E. vesicularis, A. verditer* and *Habrocytus* sp. – limited their attack exclusively to those larvae which had spun cocoons in the foliage. Other species – *A. lophyri* and *A. indistincta* – were obtained only from cocoons from soil samples. *D. diprionis* was obtained from cocoons from both soil and foliage samples. *E. subclavatus* was not found in 1954, but it was the only species obtained from cocoon samples in 1955 (soil samples only).

The abundance of "cocoon" parasites at Great Cloche is shown in Table III. Abundance is expressed both as the number of parasites per square foot and as the percentage of sound cocoons parasitized in order to show that, although the proportion of parasitism in both soil and foliage samples in 1954 was similar, the number of individuals involved in the foliage samples was considerably less than in the soil samples. The most important species in 1954 both in soil and foliage samples was *D. diprionis,* this parasite being responsible for more than half the parasitism in both micro-habitats.

Discussion

Considerable variability was found in the parasitism of *N. p. banksianae*, especially in the earliest and latest immature stages. Egg parasitism was absent in the Great Cloche outbreak, but present at Nairn Centre in two of the three years studied. The incidence of egg parasitism was low, but it would be very unwise to attribute even the small amount found to the one species for which identification was obtained, especially since no relation between emergence holes and immature parasites could be established.

The proportion of feeding stage larvae attacked by parasites ranged from 9.1 to 28.9 per cent, and did not show any consistent differences between the two areas studied (Table I). Six of the 11 species obtained were generally responsible for the greatest portion of parasitism, although the relative abundance of these species varied from year to year. Occasionally, however, another species became abundant temporarily, as at Great Cloche in 1955 when an otherwise rare species of *Lamachus* accounted for over 20 per cent of parasitism (Table II).

The difference in parasitism between two years' samples of cocooned larvae at Great Cloche was striking. Six species were obtained in 1954, but none of them was present in 1955. The absence of three of these species in 1955 can be explained by the absence of cocoons in the ground-cover foliage, since *A. verditer*, *E. vesicularis* and *Habrocytus* apparently confine their attacks on *N. p. banksianae* to cocoons spun in foliage. The replacement of the other three species obtained in 1954 by a single, different, species in 1955 cannot be explained with information at hand. However, in spite of this striking difference in the species complement, the overall parasitism, expressed as the percentage of sound cocoons parasitized or the number of parasites per square foot, was not greatly different, being 35.7 per cent and 0.50 per square foot in 1954 and 38.3 per cent and 0.40 per square foot in 1955 (Table III).

Much remains to be learned about the parasites of this sawfly. It is not known which of the 18 species obtained in this study were acting in a primary capacity, and which in a secondary capacity. Further, when one considers that the 11 species attacking feeding stages and the seven obtained only from cocooned larvae are all present in the "cocoon" stage, it is clear that *N. p. banksianae* forms a fruitful field for a study of the interaction of parasite species on a single host.

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Estimation of Adult Populations of the Larch Sawfly, *Pristiphora erichsonii* (Htg.)[1]

By W. J. Turnock[2]

This paper is one in a series on techniques for estimating populations of various stages of the larch sawfly (Ives, 1955; Ives and Prentice, 1958; Ives and Turnock, 1959) to provide a basis for the evaluation of mortality factors. The larch sawfly overwinters in a cocoon in the soil and adults emerge during the spring and summer (Turnock, 1960). This paper describes the methods and results of sampling adults as they emerge from the soil.

Methods

Emergence cages (Turnock, 1957) with a sampling area of two square feet were used to trap the adults as they emerged from the soil. Data were collected from one plot for four years and another plot for one year to test the technique at different population levels of the larch sawfly.

Plot I was located in the Whiteshell Forest Reserve, Manitoba, and has been described in an earlier paper (Ives and Turnock, 1959). This plot was divided into four sampling areas, each measuring 0.5 by 2.5 chains or 0.125 acres. Annual rotation of the sampling areas was necessary to minimize damage to the moss surface from trampling. An analysis of variance showed no significant differences in stand density between the sampling areas or in sawfly populations within the sub-plots. Each year 100 emergence cages were located at random within the sampling area.

Plot II was located in a pure tamarack stand in the Agassiz Forest Reserve, Manitoba. The stand was younger and denser (1,450 stems per acre) than in Plot I, and about one-third of the ground surface was flooded throughout 1959, which was the only year of sampling on this plot. The sampling area measured 0.5 by 2.0 chains or 0.1 acres, and 70 locations for sampling units were selected at random throughout the sampling area. Of these locations, only 39 were on ground that lay above the water table, and 31 locations were under water throughout the summer. Emergence from the latter was assumed to be zero and emergence cages were established only on the 39 locations that lay above the water table.

Results

Bases for stratification

Stratification of soil sampling units on the bases of crown cover and topography led to improved efficiency in the estimation of cocoon populations. The same classifications were tested with the adult emergence data. The distances from the crown periphery to the centres of the emergence cages in each of the three crown cover categories were:

Under crown – more than nine inches
Edge of crown – from nine inches inside to nine inches outside
Outside crown – more than nine inches

The classification of topographic locations into three categories, hummocks, intermediates, and depressions, was based on the relative levels of the ground surface. Table I shows the average number of adults per cage and the number of sample units for each stratum in Plot I from 1956 to 1959.

Constants were fitted to the data for each year to test for interaction but no significant F values were obtained. In Plot I an analysis of variance gave F

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TABLE I

Distribution of the mean number of adults per sampling unit in relation to crown cover and topography from 1956 to 1959. Number of sampling units in brackets.

Year	Crown cover classification	Topographic Classification			
		Hummock	Intermediate	Depression	Totals
1956	Under	3.09 (11)	2.00 (2)	2.40 (5)	2.8 (18)
	Edge	3.20 (10)	1.94 (18)	0.50 (2)	2.3 (30)
	Outside	2.35 (17)	2.42 (26)	1.19 (9)	2.1 (52)
Total		2.79 (38)	2.22 (46)	1.19 (16)	2.27
1957	Under	12.64 (11)	8.73 (15)	6.75 (4)	9.9 (30)
	Edge	14.67 (9)	12.53 (15)	1.00 (2)	12.4 (26)
	Outside	10.78 (9)	7.19 (26)	4.44 (9)	7.4 (44)
Total		12.69 (29)	9.04 (56)	4.60 (15)	9.43
1958	Under	8.36 (11)	7.41 (17)	2.67 (3)	7.3 (31)
	Edge	4.22 (9)	6.50 (6)	6.25 (4)	5.4 (19)
	Outside	6.00 (13)	6.95 (22)	3.33 (15)	5.6 (50)
Total		6.30 (33)	7.07 (45)	3.77 (22)	6.09
1959	Under	9.25 (12)	6.56 (9)	0 (1)	8.1 (21)
	Edge	6.00 (13)	3.60 (10)	1.00 (4)	4.4 (27)
	Outside	4.58 (19)	3.12 (26)	0.67 (6)	3.3 (52)
Total		6.27 (44)	3.91 (45)	0.73 (11)	4.60

values for differences between categories in crown cover and topographic classes, each with two and 77 degrees of freedom, as follows:

Year	F value	
	Topography	Crown cover
1956	3.25*	0.68
1957	3.45*	1.39
1958	3.48*	0.88
1959	42.04**	18.54**

The importance of topography as an influence in the distribution of adult emergence is indicated in all four years. Crown cover apparently did not influence the distribution of adult emergence except in 1959. The annual sampling areas were uniform when the plot was established in 1955 but since that time the tree crowns have suffered considerable branch mortality and some trees have died. Thus the distribution of larch sawfly cocoons in the ground was affected when the degree of the crown closure declined. In 1955 there were 114 trees in the 1958 sampling area but only 105 remained to support the larch sawfly population that gave rise to the 1959 adults.

These results indicate that stratification on the basis of topography should give increased accuracy in 1956, 1957, and 1958 while in 1959 stratification by both topography and crown cover should be justified. In Plot II the degree of crown closure was over 90 per cent so no stratification on this basis was attempted. The high water table made the topographic categories used in Plot I untenable so two new categories for classifying the sample units were set up:

1. Flooded – water table within ½ inch of the ground surface
2. Dry – water table more than ½ inch beneath the surface

When the data were tested with analysis of variance the difference between categories was highly significant ($F = 9.13$ with one and 68 degrees of freedom).

Therefore, stratification of the sample units on the basis of topography should increase the accuracy of the population estimate in Plot II.

Estimation of adult populations

The emerging adult populations were estimated from the total number of female larch sawflies recorded in the emergence cages. On the basis of random sampling units the estimated population, standard deviation, and 95 per cent confidence interval for each annual sampling area were:

Plot	Year	Number of adults	Standard deviation	95% confidence interval
I	1956	6,180	555.39	$5{,}078 < \mu < 7{,}282$
	1957	25,673	2,113.97	$21{,}479 < \mu < 29{,}867$
	1958	16,580	1,185.93	$14{,}227 < \mu < 18{,}933$
	1959	12,524	1,194.96	$10{,}153 < \mu < 14{,}895$
II	1959	1,338	409.70	$521 < \mu < 2{,}155$

Estimates were also made on the basis of stratified sampling units. With the exception of the data for Plot I, 1959, stratification reduced the standard deviation by less than four per cent, an increase in efficiency too small to justify its use. In Plot I, 1959, stratification reduced the standard deviation by 25.15 per cent. The estimated population, based on stratified sample units, was 10,325; standard deviation 894.38; and 95 per cent confidence interval $8{,}550 < \mu < 12{,}100$.

The ½ - 95 per cent confidence intervals gave the following percentages when divided by their respective means:

Plot	Year	Type of sampling	$\frac{100 \lvert d \rvert}{\mu}$
I	1956	Random	17.8
	1957	Random	16.3
	1958	Random	14.2
	1959	Stratified	17.2
II	1959	Random	61.1

On this basis the population estimates were statistically satisfactory for Plot I but not for Plot II. From another standpoint, however, the degree of accuracy attained in Plot II may be regarded as acceptable because the mean was estimated with 95% confidence to plus or minus 817 adults. It is possible that no better accuracy can be attained in estimating a small population in a variable environment. Some improvement in the estimate may be attained in the future by careful examination of the topography and water level fluctuations in the plot leading to better stratification of the sampling units.

Summary

Adult larch sawfly populations in a dry, pure, tamarack stand were estimated. Annual populations of emerging larch sawfly adults were estimated with satisfactory accuracy in a plot 0.125 acres in area with 100 two-square-foot cages. The use of sampling units stratified on the basis of topography was not justified except where the degree of crown closure was reduced to the point where strata based on crown cover and topography could be used. Similar stratification would probably be justified in stands containing other tree species.

The second plot had a very low larch sawfly population and the ½ - 95 per cent confidence interval was high in relation to the mean. As this interval was only 817 adults the population estimate might still afford an adequate basis for the study of mortality factors. The high water table made large areas within

this plot completely unsuitable for the survival of larch sawfly. The accuracy of population estimates might be increased by more careful stratification on the basis of topography.

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Notes on *Matsucoccus macrocicatrices* Richards (Homoptera: Margarodidae) and its Association with *Septobasidium pinicola* Snell in Eastern Canada[1]

By W. Y. Watson[2], G. R. Underwood[3], and J. Reid[4]

Three known species of scale insects belonging to the genus *Matsucoccus* occur on pine trees in northeastern North America: *M. gallicolis* Morr., on pitch pine, *Pinus rigida* Mill., and scrub pine, *Pinus virginiana* Mill. (Parr, 1939); *M. resinosae* Bean and Godwin on red pine, *P. resinosa* Ait. (Bean and Godwin, 1955); and *M. macrocicatrices* Richards on eastern white pine, *P. strobus* L. (Richards, 1960). This last species, in contrast with the others, is closely associated with the fungus *Septobasidium pinicola* Snell. From 1957 to 1959 personnel of the Forest Insect Laboratory, Sault Ste. Marie, and the Forest Biology Laboratory, Fredericton, collected some 500 specimens from 21 areas in Ontario and the Maritime Provinces. These collections, augmented by herbarium specimens provided by the Forest Pathology Laboratory, Maple, from five other areas in Ontario, provided not only the insect specimens necessary for the description of the species, but information on its biology and distribution.

Fungus collections were made either randomly or at two-week intervals from early May until mid-September. Each fungal mat with a small portion of the bark was removed from the tree and sent to the laboratory where the insects were removed for storage in 70 per cent alcohol. Further information on the biology was obtained by the use of metal, salve-tin cages (Fig. 1) placed over the fungal mats and caulked to prevent insects from moving into or away from the isolated fungus. These cages were removed periodically, and the fungus and caulking compound were thoroughly examined for insects.

The insect and its associated fungus were found in 26 areas in Ontario and the Maritime Provinces (Fig. 2). In New Brunswick specimens were collected along the Southwest Miramichi River Valley, and along the St. John River Valley southeast of Fredericton, and in Nova Scotia from Queens County in the south to Inverness County in the north. In Ontario the collections were from the south central part of the Province, from Miller Township, Frontenac County, in the south to Mattawa in the north.

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Fig. 1. Salve-tin cage used to isolate individual fungi.

The Fungus

In eastern North America *S. pinicola* is restricted to eastern white pine (Couch, 1938). In the present study, the brown, roughly circular fruiting bodies (Fig. 3), varying from less than one half inch to more than two inches in diameter, were found on trees from one to nine inches d.b.h. and from 10

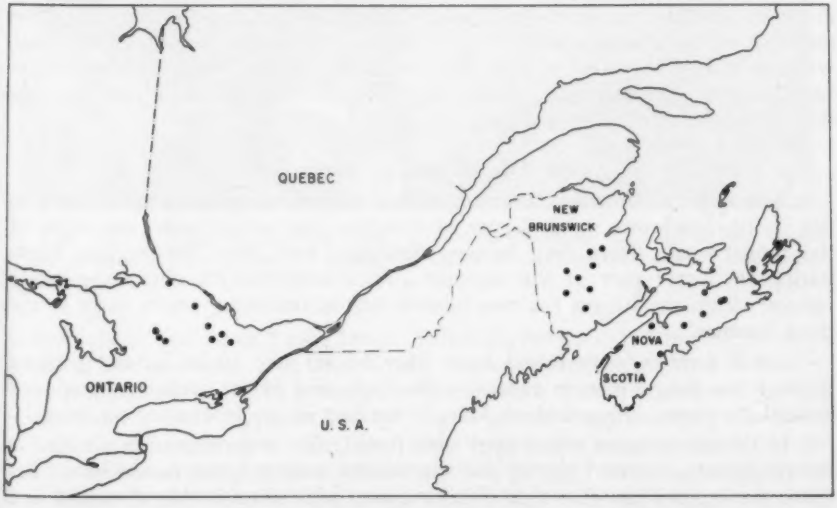


Fig. 2. Collection points of *Matsucoccus macrocicatrices* Richards and *Septobasidium pinicola* Snell.

Fig. 3. Fruiting body of *Septobasidium pinicola* Snell.

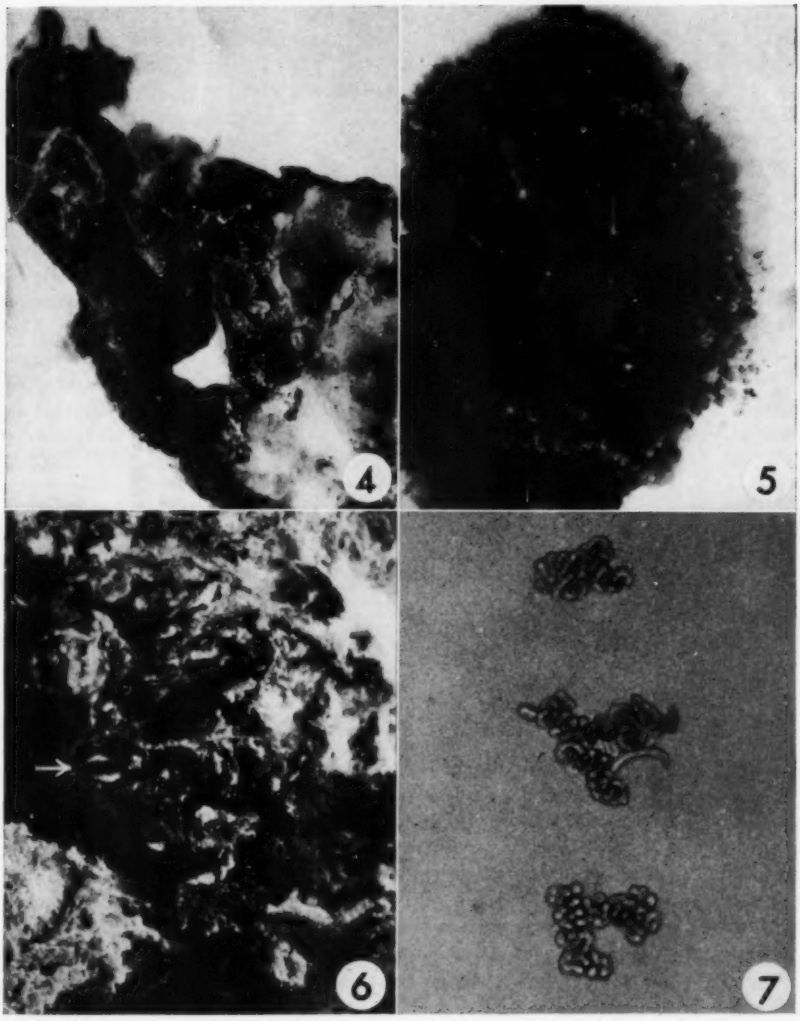
to 30 feet high. The outer, ragged fringe of the fungus is pale and thin in contrast to the thick, older growth. Frequently a grey-green lichen grows from the upper surface of the fungus. Fungal mats were common on the smooth bark of the lower trunks, and rare on the branches. Affected trees were found in over-stocked stands containing more than 60 per cent white pine, growing in moist, shaded areas where the canopy was almost or quite closed. At most locations in Ontario the fungus was present on about one-quarter of the trees, whereas at two locations in New Brunswick the fungus was present on about half the trees. At Boiestown, N.B., the average number of fungal mats per tree was 17, but in other areas the fungus appeared to be less common.

The Life History of the Insect

The eggs of *M. macrocicatrices*, laid in lichens or crevices in the bark in late spring, hatch into motile larvae, or crawlers, that gather under the edges of the fungal mats. Here they become stationary and form intermediate stages during the latter part of the summer. These intermediate stages apparently remain within the fungus for two winters before becoming adults early in the third summer.

Adult females were found from May 15 to July 30 in lichens growing through the fungal mat, in cracks in the bark, and in the caulking compound around the cages. Eggs laid on May 27 hatched in the laboratory on June 11.

In the one instance where eggs were found, they were massed in a cavity in the thallus of a lichen (Fig. 4) and surrounded with a white flocculence. Because the females are obviously able to move quite considerable distances, and because so few eggs have been found, it is probable that most of them are laid in sheltered places in the bark or under bits of debris. Each egg is ovoid,



Figs. 4-7. 4, Adult female with eggs. 5, Crawlers beneath the edge of the fungus. 6, Intermediate stages embedded in fungus. 7, Coiled structures from body of intermediate stage.

pearly yellow, and about 1 mm. long. Yellowish-brown crawlers (Fig. 5) were found as late as August 7 in Ontario and August 13 in the Maritime Provinces. They congregate in jumbled masses, often of more than 100, under the edges of the fruiting body, apparently occurring in greater numbers along the lower part of the circumferance. The size of the fungal mat is not indicative of the number of insects found therein, smaller mats frequently harbouring more insects than larger mats. Soon after the crawlers begin to feed, they moult and become legless intermediate stages. These intermediate stages were found in almost all the fungal mats examined. Newly-formed intermediate stages slightly smaller

and cleaner than the more mature intermediate stages, were first found in early August in fungal mats which frequently contained older living intermediate stages. The dark brown or black, waxy, spherical bodies (Fig. 6), with their stylets inserted in the bark of the tree, may be located near either surface of the fungus, having been enveloped gradually by the growth and thickening of the fungus.

The presence of living immature stages in the fungal mats at all times of the year, and the rather limited span of other stages, suggests that there may be a two-year life cycle, the overwintering stages being the immature and mature intermediate stages. If this is so, *M. macrocicatrices* differs from *M. gallicolis*, which has a one-year life cycle and overwinters as an egg (Parr, 1939), and from *M. pini* (Greene) and *M. resinosae*, which are bivoltine and overwinter as first-stage larvae (Bean and Godwin, 1955).

Males were not found, suggesting that this species is parthenogenetic, as is *M. pini* of Europe (Bean and Godwin, loc. cit.). No parasites were discovered. Some of the fungal mats yielded dead, hollow intermediate-stage shells that had apparently not resulted from parasitism.

Insect-Fungus-Host Relationships

The relationship between *M. macrocicatrices* and *S. pinicola* is not fully understood, nor is the relation of the insect-fungus partnership to the host. Undoubtedly the fungus protects the insect from adverse weather conditions, and possibly also from parasitism. The epiphytic nature of the fungus (Snell, 1922), and the finding of haustoria-like structures (Fig. 7) in the body cavity of the intermediate stage insects, as well as the presence of hollowed-out intermediate-stage shells strongly suggests that the fungus may infest and derive nourishment mainly from the insect. If this is so then the relationship between the insect and fungus is mutually beneficial or symbiotic, closely resembling that between *S. burtii* Lloyd and *Aspidiotus osborni* New. and Ckll. described by Couch (1938). The evidence here seems to indicate a much less complex relationship than exists between other species of *Septobasidium* and their insect partners. The escape of the female insects before laying eggs or bearing young, and the aggregating of the crawlers beneath the edges of the scale rather than being caught in specific 'traps', suggest a less dependent association between *S. pinicola* and *M. macrocicatrices*. There is, however, no indication that either member of the partnership is able to live independently of the other.

Because of the close relationship between the insect and the fungus, it is difficult to assess their relative effects on the tree. Since there is no evidence of direct fungal penetration of the bark, it is possible that any damage sustained by the tree is caused primarily by the insect. Damage to the trees is quite localized, with no obvious disease symptoms or mortality being observed. Other species of *Matsucoccus* are known to produce gall-like swellings, discoloration, and eventually, in severe cases, death (Craighead, 1950). When the bark beneath the fruiting body of *S. pinicola*, was removed a depression or irregularity (Fig. 8) with the shape of the fungus, could be seen on the wood. Occasionally, if the bark was dead or dying beneath the fungus, the wood was stained. Brownish, pitch-filled areas, similar to those described by Parr (1939) for *M. gallicolis*, were sometimes found beneath the fruiting body.

Summary

Observations of the biology, distribution, and insect-fungus relationships of *M. macrocicatrices* are presented. The closely associated fungus and insect are

Fig. 8. Depression in wood beneath the fungal mat.

found in central Ontario and the Maritime Provinces on white pine. It is suggested that the insect has a two-year life cycle, and that its relationship with the fungus is symbiotic. Damage to the host tree is negligible.

Acknowledgments

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Developmental Rates of Larch Sawfly (*Pristiphora erichsonii* (Htg.)) Larvae in an Insectary and in Field Shelters[1]

By W. G. H. Ives[2]

In 1959 a study was conducted in the Whiteshell Forest Reserve, Manitoba, to determine if insectary-reared larch sawfly larvae developed at the same rate as in the field. Data were collected on the rate of frass production in both situations and used as an index of larval development. This was part of a broader study that will be reported on more fully in a later publication, but the immediate results should be of interest to those concerned with studies on ecological life histories of other insects.

Methods

Description of coprometer

Coprometers were designed to collect frass from two colonies of larvae for fixed time intervals (Fig. 2). They were similar in principle to those designed by Green and Henson (1953) but were of heavier construction and designed to operate for one-week periods. The turntable (A) holding the collecting vials was powered by a phonograph motor (B) with the governor removed. The governor bearings and shaft were used as the pivot for the escapement mechanism (C) which was operated by two solenoids (D). A clock (G) with an eight-day movement provided the timing mechanism and a six-volt lantern battery (F) was used as the power source.

A schematic diagram of the apparatus is shown in Fig. 1. Two pairs of electrical contacts (H) were located on the face of the clock. A piece of springy brass was soldered to the hour hand (I), which was grounded to the

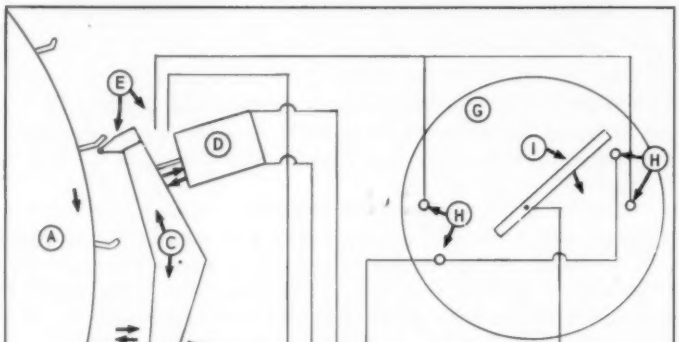

Fig. 1. Schematic drawing of coprometer (see text for explanation of labels).

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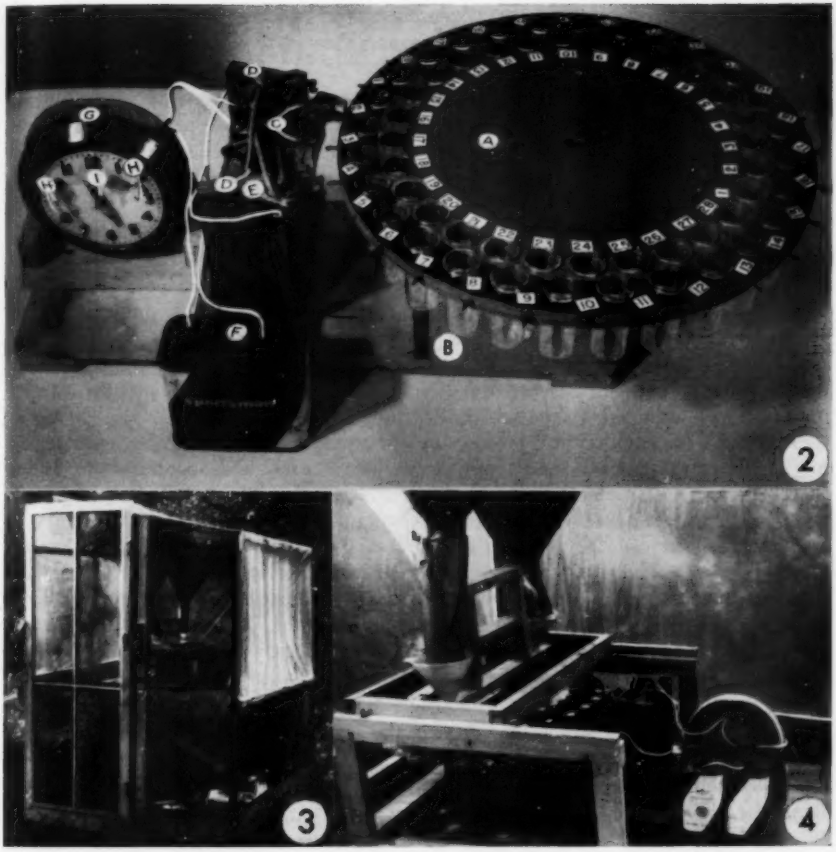

Figs. 2 to 4. Equipment used in study of frass production. Fig. 2. Coprometer (see text for explanation of labels). Fig. 3. General view of one of field shelters. Fig. 4. Coprometer in operation in a field shelter.

battery. Movement of the hour hand completed this part of the circuit twice every six hours, advancing the turntable one position during this period. Additional contacts (E) made of springy brass were located near each end of the escapement mechanism. A copper "U" on each end of the rocker arm of the escapement mechanism served as the breaker. The circuits were arranged so that when electrical contact by the hour hand activated one solenoid, the movement of the rocker arm cut the power supply to that solenoid by opening the switch at the other end of the rocker arm. At the same time the switch nearest the solenoid was closed and the sequence was repeated by the other solenoid when the hour hand touched the next contact.

Experimental procedure

The insectary used in this study had overhanging eaves and was well ventilated by 16-inch strips of copper screening beneath the eaves and at floor level. It was butted to another building at the west end, and was thus protected from direct afternoon sunshine. In the insectary, the insects were reared on

twigs inserted in water in well ventilated plastic rearing cages. A hole in the bottom of the rearing cage was placed over a funnel to direct the frass into the collecting vials on the coprometer.

Field shelters to protect the coprometers were built over the tops of small tamarack trees bent to a workable height (Fig. 3). The upper part of a light wooden framework was covered with clear polyethylene film extending down to the level of the table supporting the coprometer. The north side and the lower parts of the other three sides were screened to exclude wasps and hornets. Access was through a screen door on the north side. In the shelters the insects were reared on two separate groups of branches, centred over funnels leading into the appropriate holes in the coprometer turntable (Fig. 4).

Larch sawfly eggs for field rearing were obtained by caging female sawflies on twigs in the shelters, while those for insectary rearing were obtained from simultaneous caging of females on nearby trees. After two days the eggs for insectary rearing were collected and observations on development begun. Larval material was obtained from field collections sorted by instars. The larvae in each instar were divided into two groups of similar age. One group was reared in the insectary, the other in the field shelters. First and second instar larvae were divided on a colony basis to avoid injuring the larvae. Colonies of third and fourth instar larvae were divided when necessary to obtain two groups of similar age composition. Larvae for insectary rearing were established by inserting a twig bearing larvae into water with additional tamarack foliage. Larvae for field rearing were established by placing the larvae-bearing twigs in small vials containing water, stoppered with cotton batting. The twigs and vials were then clipped to branches in the shelters. The foliage on the larvae-bearing twigs remained fresh until the larvae became established on the branches. All rearings were continued until feeding was complete.

Thermograph records were taken in the insectary and in a Stevenson screen in one of the field shelters. Another Stevenson screen was placed in full sun near the shelters and periodic thermograph records taken to compare with those from the shelter.

At the peak of the rearing program six coprometers were used, three in the insectary and three in the field. The vials for collecting frass were changed once a week. A desiccating cabinet was used to remove excess moisture from the frass prior to storage. The frass was then sorted and all debris removed, dried at 105° C for 48 hours, and weighed to the nearest 0.2 milligrams.

Results

Temperature comparisons

The daily air temperature courses in the insectary, in a field shelter and in the field are shown in Fig. 5. The figure also shows the approximate amount of cloud cover at 0800, 1000, 1200, 1500, and 1800 hours on each of these days. During predominantly cloudy weather the temperature curves for all three locations were similar (Fig. 5B – entire curve, and Fig. 5E – 1000 to 1300 hours). During periods of light or intermittent cloud cover the pattern changed considerably. Temperatures in the field shelter and in the field agreed fairly well. On sunny days there was a slightly higher maximum temperature in the shelters, and a small time lag, but the shape of the two curves was very similar. However, the temperature course in the insectary was noticeably different, with much less diurnal-nocturnal fluctuation.

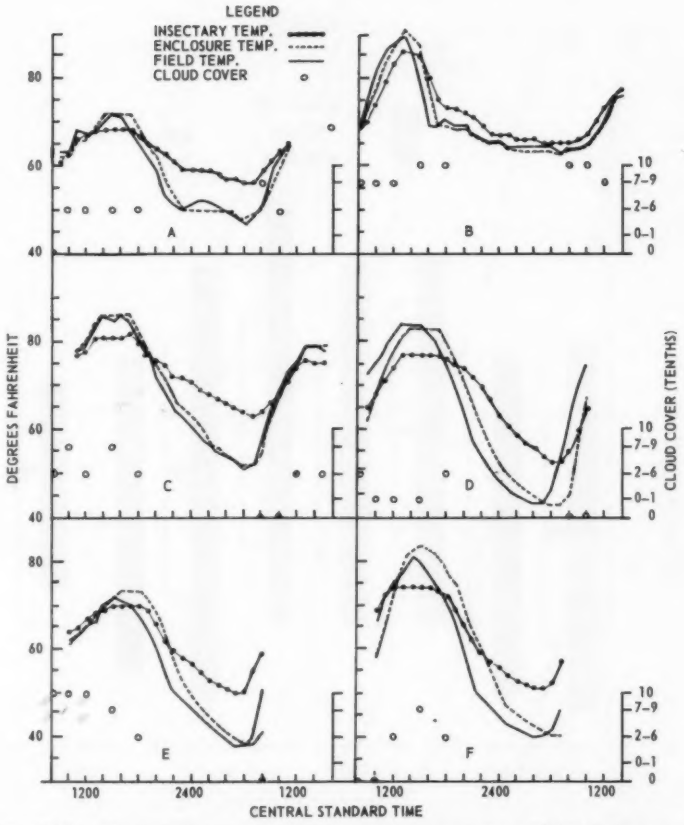

Fig. 5. Daily air temperature courses in an insectary, in a field shelter, and in an exposed field location, with cloud cover at 0800, 1000, 1200, 1500 and 1800 hours. A — 0900 hours, July 9, to 1100 hours, July 10; B — 0800 hours, July 14, to 1400 hours, July 15; C — 1100 hours, July 16, to 1500 hours, July 17; D — 0900 hours, July 18, to 1000 hours, July 19; E — 1000 hours, August 6, to 0800 hours, August 7; and F — 1000 hours, August 7, to 0700 hours, August 8.

The means of daily maximum, minimum and mean (12 readings at two-hour intervals) air temperatures for one-week intervals from June 29 to August 24, 1959 in the insectary and in the field shelter are shown in Fig. 6. The mean of daily means was usually one or two degrees higher in the insectary than in the field shelter. Mean minimum temperatures were consistently lower in the shelter than in the insectary, while the mean maxima were higher. Consequently, larvae in the field were subjected to a much wider range in temperatures than in the insectary.

It is concluded from Fig. 5 that a satisfactory approximation of field temperatures is given by temperatures in the field shelters, with one exception. On July 28 the high temperatures in the field shelters caused heavy larval mortality in all stages. The thermograph registered its limit of 100°F., but the actual temperature was probably higher. Because of this mortality, none of the comparisons in the following section include results from rearings in progress on July 28.

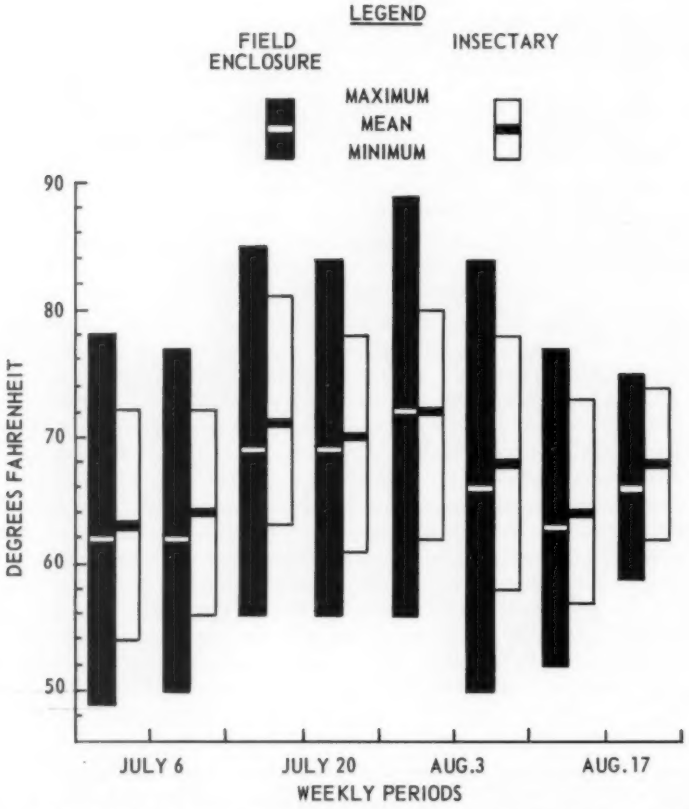

Fig. 6. Means of daily maximum, minimum, and mean air temperatures for one week intervals from June 29 to August 24, 1959, in an insectary and in a field shelter.

Cumulative frass production

The cumulative percentages of total frass collected in the insectary and in the field shelters are shown for 10 paired rearings in Fig. 7. No consistent differences between the two types of rearings were evident. The gap in Fig. 7C was caused by a temporary food shortage in the insectary rearing, but the larvae apparently recovered. There appears to be a real difference in the curves in Fig. 7B, possibly due to an initial difference in the ages of some of the larvae. As only small numbers of larvae were involved in this experiment (about 12 in each group) minor age differences could have been important. The remaining deviations do not appear to be due to temperature differences. Figs. 7D, 7F, and 7H show the frass production of larvae reared between July 13 and July 27, and Fig. 7G between July 16 and July 27. All of these larvae were exposed to the same temperature conditions throughout most of the feeding period. The curves in Fig. 7D are almost identical, while noticeable deviations occur in Figs. 7F, 7G, and 7H. Similarly, the larvae producing the frass shown in Figs. 7J and 7K were reared between August 6 and 17, and August 10 and 22 respectively. They would also be subjected to the same temperatures during the period when the deviations occurred. In Fig. 7J development in the insectary was slightly

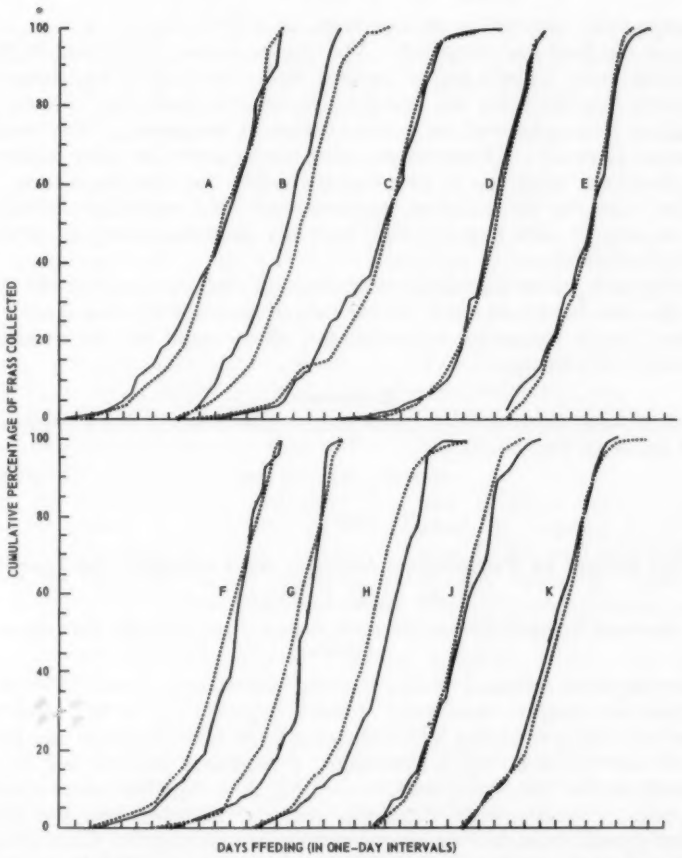

Fig. 7. Cumulative percentages of frass collected from larvae in field shelters (solid lines) and in an insectary (dotted lines): A — second instar larvae June 29; B — third instar larvae August 6; C — eggs June 29; D — first instar larvae July 13; E — fourth instar larvae July 6; F — first instar larvae July 13; G — second instar larvae July 16; H — third instar larvae July 13; J — fourth instar larvae August 6; and K — fourth instar larvae August 10.

faster than in the field shelter, while the converse was true in Fig. 7K. The differences were therefore probably attributable to slight initial age differences, to differential lodging of the frass on the foliage, or to a combination of the two.

It is therefore concluded that the rate of development in the insectary was essentially the same as in the field shelters, and that any differences which occurred in this study were due to differences in age composition of the two groups of larvae or to differences in the amount of frass lodging on the foliage. Because temperatures in the field shelters approximated field conditions, it was unlikely that field development differed appreciably from that recorded in the field shelters.

Summary

A coprometer designed to run for one-week intervals is described.

Temperature courses in an insectary, in a field shelter, and in a sunny position in the field are compared. The curves in the shelter and in the field were similar with slightly higher maxima and a small time lag, especially on sunny days, but those for the insectary fluctuated much less. Larvae in the field shelter were subjected to a wider range in temperature fluctuation than those in the insectary. However, the mean air temperatures were similar, those for the insectary being one or two degrees higher than for the shelter. It was concluded that the field shelters approximated field conditions satisfactorily, except on July 28. On that day high mortality occurred among all larval stages in the field shelters.

Comparison of the cumulative percentage of frass produced in the insectary and in the field shelters showed that the rate of development was similar in both situations. Some deviations occurred, but these could not be attributed to temperature differences.

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The Effect of Population Density on Fecundity in Insects

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Four steps are necessary in constructing and utilizing a mathematical model for control of a specific insect pest. First, a large volume of field data must be collected according to a plan which is sound from both statistical and biological points of view (Morris, 1955). Secondly, a suitable procedure for developing component parts of the whole model and fitting these together must be developed (Watt, ms.). Thirdly, after exhaustive study of available data and testing of equations against these data we must determine the appropriate form of equation to express the action of each type of phenomenon governing dynamics of the pest population. This paper and other in the series (e.g., Watt, 1959) are designed to obtain such formulations. Which phenomena are worthy of study for a given pest species will become clear through mathematical analysis of life-table data of the type collected by Morris and Miller (1954). Finally, parameter values are obtained from the data and the equations are manipulated to determine optimum control practices, using methods outlined by Watt (ms.).

For a mathematical equation to be suitable as a description of a biological phenomenon, it must meet certain desiderata. First, the equation must provide a statistically satisfactory fit to data collected on the phenomenon. Secondly, it should be no more complex than is necessary to provide such fit. Thirdly, it ought to incorporate insight into the biological mechanism of the phenomenon it describes. Finally, the equation must be general, in that it can be made to reproduce any set of measurements on the phenomenon (allowing, of course, for sampling error), merely by altering parameter values. In short, the equation should be steeped in, and a product of, the lore and data of biology. The formula specifically should not have been selected for any of the following reasons: purely a priori considerations; ease of mathematical manipulation; it gave a good fit, regardless of its meaning; it provided a convenient analogue with mathematical thinking in another subject-matter field, such as physics.

It is my hope that the present series of papers will not only be useful to biologists, but also to the increasingly large group of mathematicians and statisticians studying biological material. Animals are not beans in a bean bag, gas molecules, or abstract spheres; any attempt to treat them as such will result in unrealistic equations which are not only useless to the biologists, but which can mislead them, and have often misled them, since they may not understand completely the assumptions on which the formulae were based. Two important facts must be faced, and appropriate measures taken, by anyone developing mathematical models describing the behavior of populations of animals. First, animals are subject to all kinds of inherent limitations imposed by their biological nature. (They have limited range of perception, limited egg supply, limited capacity for food each day, and limited distance they can move each day, etc.). Secondly, one of the most striking features about animal populations is the ubiquitous and enormously important role played by competition in all its guises: competition for food, oviposition sites, interference, cannibalism, etc.

When we come to examine the literature on mathematical models describing the effect of population density on fecundity, we find these publications fall into three categories.

The first group follow Lotka (1923), and Volterra (1926), who independently treated reproductive rate (the number of offspring per head per unit time) as if it was a constant. However, Lotka, unlike many of the writers who followed him, conceded in a phrase immediately below his equation (1) (1923), that it was probably not correct to do this, since the coefficient of birth rate is in general a function of population density. Mathematicians would have been well-advised to consider an early warning of Stanley (1932). He asserted, "The writer feels that some criticism may be levelled against Volterra's work on the grounds that so many assumptions have been made in order to simplify the mathematical treatment that the entities considered can nowhere be found in the roster of living organisms". Bartlett (1957) stated, "Criticisms from biologists of the mathematical work of Lotka (1925), Volterra (1926) and subsequent writers on the growth and interaction of biological populations have, however, sometimes been justified and sometimes unjustified, for in spite of inevitable limitations such work constitutes a permanent contribution to the understanding of how populations may behave". Lotka, Volterra, Bailey (1931), Nicholson and Bailey (1935), Kostitzin (1939), Feller (1939), Kendall (1948), Chiang (1954), Wangersky and Cunningham (1956), Leslie (1957, 1958) and Bartlett (1957), all made the assumption that reproductive rate is a constant. Rich (1956) assumed that fecundity was constant, but proved by his own experiments that this assumption was false.

The second group of equations used to describe the effect of density on reproductive rate might be called empirical formulas, in that they were used largely because they provided good fits to the data. Pearl and Parker (1922) used such a formula, but it did not fit the data of Utida (1941a), and hence lacked generality. Andersen (1957) used another such empirical formula.

The third group of equations is designated to incorporate insight into the mechanism by which density governs fecundity. Pearl (1932) proposed a formula in which "The orderly change in rate of egg production with increasing density is shown to be described by the same type of mathematical equation as that which relates mean free path of molecules to density in a gas". However, molecules are never faced with the problem of finding mates, and hence the equation which is applicable for molecules is inadequate to describe the effect of population density on reproductive rate, as will be brought out subsequently in

this paper. The second formula intended to describe this mechanism was derived by Fujita and Utida (1953) from the logistic equation of population growth. However, the latter equation has been shown to be unsupportable by empirical data (see, e.g. Wright, 1926; Feller, 1940; Smith, 1952; Andrewartha and Birch, 1954; Slobodkin, 1954; Watt, 1955, and other papers discussed hereinafter). Fujita and Utida tested six bodies of data and got good fits. However, Fujita apparently discovered very quickly that the formula lacked generality, because in 1954 he published a new equation describing the effect of density on fecundity. This paper presented a model which is the most realistic yet devised to describe the effect of density on fecundity. However, Fujita never performed tests to demonstrate that his equation fitted data, apart from showing that it could simulate the results obtained from various experiments.

Hence the current situation with respect to mathematical models describing the effect of population density on fecundity appears to be as follows. All but one of the available models can be shown to be unrealistic, or to lack generality. On the other hand, the one model which appears to meet the criteria of being realistic and general has never been proved to meet them. In view of this situation, one more paper attempting to finalize discussion about this subject seems justified. Furthermore, since a model is only as useful as it is general and realistic, an exhaustive and critical review of the literature, followed by presentation of results from model tests also seems justified. It will be shown that Fujita's equation is not in accord with the facts; hence a new model will be developed and tested, and its implications discussed.

Review of Empirical Findings

Pearl and Parker (1922), using *Drosophila melanogaster* Meig. in bottles, were the first to study the effect of density on the reproductive rate of laboratory insect populations. The variables they measured were "mean population average —16 days" and "imagoes per mated female per day". Their data are plotted in Fig. 1. Since the dependent variable they counted is the number of imagoes, rather than the number of eggs, they were vulnerable to the criticism that the effect of density on fecundity was confounded with the effect of density on pre-imaginal survival. Following Fujita (1954), I shall use the term "*Drosophila*-type" to describe curves for population density effect on oviposition rate which appear as in Fig. 1.

Allee (1931) showed that the effect of density on reproduction rate could take a different form than the *Drosophila* type. He analyzed Chapman's (1928) data on rate of increase in laboratory populations of *Tribolium confusum* Duv. Chapman started all his cultures in 32 grams of flour, and with six initial densities of 2, 4, 8, 16, 32 and 64 adults. Allee found that the rate of increase of population per female day was greatest (after 11 days) at the second-lowest density, not the lowest, as one would expect from Pearl and Parker's results. However, to make the matter more intriguing, as time advanced, the curve for reproduction rate against density became like the *Drosophila*-type curve. Fujita (1954) has labelled the curve for Chapman's 11-day data the "Allee type", in honor of the late Warder Clyde Allee. Chapman's results are plotted in Fig. 2. Thomas Park (1932) confirmed Chapman's findings.

In 1932 Pearl met possible criticism of the earlier Pearl and Parker (1922) paper, by showing that "fecundity of *Drosophila* (eggs laid per female day) diminished with increasing density of population, just as fertility (adult progeny produced per female day) was shown to do in the earlier work". Pearl concluded that "crowding produces the observed effect on rate of egg laying

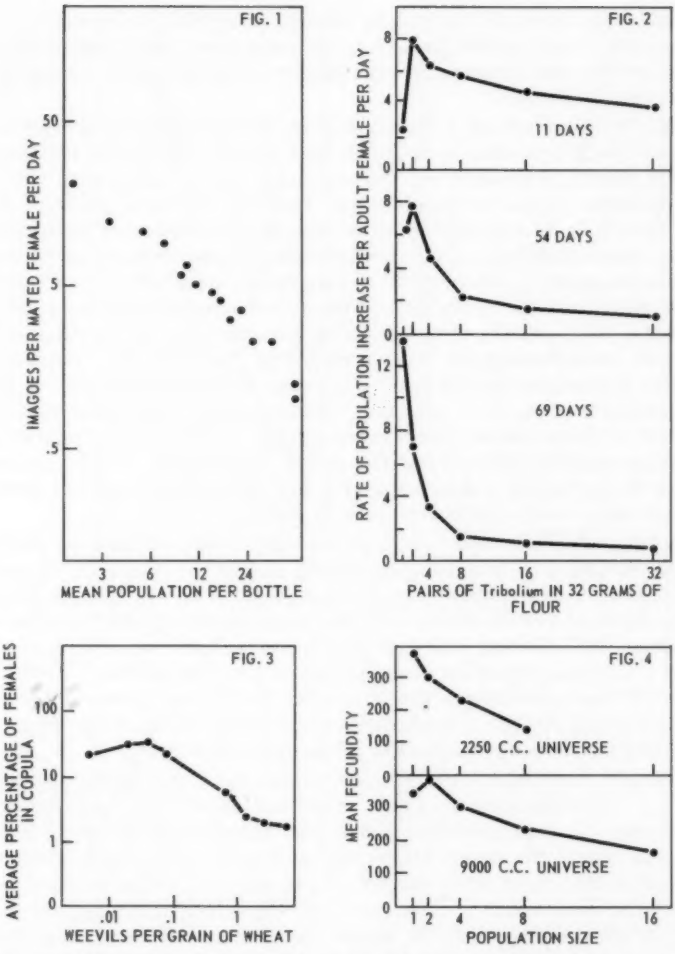


Fig. 1. The effect of population density on population growth in laboratory populations of *Drosophila melanogaster* Meig. (Data from Pearl and Parker, 1922).

Fig. 2. The effect of population density and time on the rate of population increase per female day in *Tribolium confusum* Duv. (Data from Chapman, 1928).

Fig. 3. The effect of density on copulation in laboratory populations of *Sitophilus oryzae*. (Data from MacLagan and Dunn, 1935).

Fig. 4. The effect of density and universe size on fecundity in *Dixippus* (*Carausius*) *morosus* (Data from Kirchner, 1938).

primarily, though probably not solely, as a result of a collision or interference action of the flies upon each other, which alters the normal physiological equilibrium and processes of the individual, particularly with reference to three major functions, food intake, energy output in muscular activity, and oviposition." However, examination of Pearl's (1932) Table 5 shows that his *Drosophila* in quarter-pint bottles gave an Allee-type curve.

MacLagan (1932) confirmed the existence of the Allee-type curve for the effect of density on fecundity in *Tribolium confusum* Duv. but obtained a

Drosophila-type curve for the granary weevil, *Sitophilus granarius* (L.). However, fecundity and pre-imaginal survival may have been confounded, since reproductive rate was measured as "the number of adult weevils emerging within a known period of time".

Park (1933) performed a thorough series of ingenious experiments to ascertain the mechanism producing an Allee-type curve. He found that copulation stimulated females to produce ten times as many eggs as when they were virgin, and recopulation produced an additional doubling of the fecundity. Park did not test the effect of a great number of copulation frequencies on fecundity, so we do not know the shape of the curve showing the dependence of fecundity on copulation frequency. However, he did try to assess the effect of overcopulation, and concluded from the result, that "This excludes overcopulation, to the extent here possible, as a possible factor lowering productivity rate in dense cultures." Park noted, in explaining the Allee-type curve, "In *Tribolium* populations the explanation is based, not on the optimal presence of a single item such as food, but on the interaction of two opposing factors which find their minimum of antagonism in intermediate sized initial groups." These two factors are the fecundity-stimulating effect of copulation and recopulation, which increases with density, and the fecundity-depressing effect of interference, and competition for oviposition sites, which also increases with density.

Smirnov and Wiolovitsh (1934) showed that a *Drosophila*-type curve might be due to the effect of increasing density in raising the incidence of sterility in females. They used the shield-bug, *Chionaspis salicis* L. In this instance, almost all of the depression of fecundity with increasing density could be accounted for by sterility. Smirnov and Polejaeff (1934) showed the same kind of situation with the coccid *Lepidosaphes ulmi* L., also in the Diaspididae. While in both these studies, and particularly the latter, the results are obscured by sampling error due to small volume of replication, the fact that the findings were obtained from natural populations makes them of particular interest.

MacLagan and Dunn (1935) analyzed the effect of density on *Sitophilus oryza* (L.) (Curculionidae). They performed experiments on the effect of weevil density on copulation-frequency (the average percentage of females in copula each hour); the results are plotted in Fig. 3. Also, they found that the parameters of this curve were subject to alteration by either physical or biotic factors of the environment. The curve for the effect of density on fecundity was of the *Drosophila* type. It should be pointed out here that these two Aberdeen workers were using a 1024-fold range of densities. The replicates at the highest densities used 128 weevils for every 25 grains of wheat; not many natural insect populations would ever attain densities this high. If very much lower densities had been tried, presumably curves of the Allee type might have resulted.

It was made clear by Kirchner (1938) that the *Drosophila*-type and Allee-type curves were not each peculiar to certain species. Either type can occur in any species, depending on the density of the population at the time fecundity is measured. Working with universes of three sizes, and experimental populations of *Dixippus* (*Carausius*) *morosus* (Brunn. and Redt.) (Phasmida), he obtained an Allee-type curve in the largest universe, and a *Drosophila*-type curve in the smallest universe, just as one would expect; his data are plotted in Fig. 4.

Since the *Drosophila*-type curve is characteristic of high densities for a particular insect species, and the Allee-type curve is found at low densities, then we should expect to find that a certain intermediate range of experimental densities produces an intermediate type of curve. This curve type would exhibit

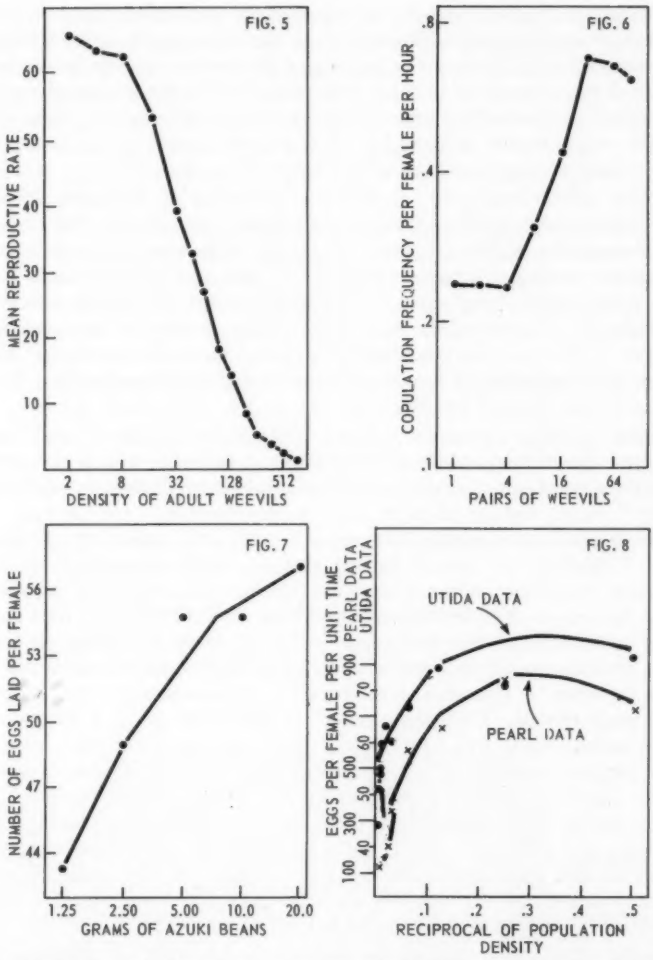


Fig. 5. The effect of density on mean reproductive rate in *Callosobruchus chinensis* (L.) (Data from Utida, 1941a).

Fig. 6. The effect of density on copulation frequency in *Callosobruchus chinensis* (L.) (Data from Utida, 1941d).

Fig. 7. The effect of competition for oviposition sites on fecundity in *Callosobruchus chinensis* (L.) (Data from Utida, 1941d).

Fig. 8. Test of Andersen's (1957) assumption that above a certain density the fecundity is a linear function of the reciprocal of density. (Data from Pearl, 1932 and Utida, 1941b).

the *Drosophila*-type falling off of fecundity at high densities, but at low densities the curve would bend towards the Y-axis, rather than appearing to become asymptotic at $(0,\infty)$. Utida (1941a) found such a curve, using experimental populations of the azuki bean weevil *Callosobruchus chinensis* (L.); his data are plotted in Fig. 5. Hereinafter, following Fujita (1954), I shall designate results such as Utida's by the term "intermediate type". In a subsequent paper, Utida (1941b) showed that an environmental factor, relative humidity, could change the parameters of the curve expressing the dependence of fecundity on density.

Utida (1941d) performed analytic experiments to determine the role of copulation frequency, cannibalism, collision, etc., in the causal pathway by which density regulates fecundity. His data for the effect of density on copulation frequency are plotted in Fig. 6. Utida (1941a) also concluded that the rate of egg production depended on the surface area of the beans available for oviposition, not the space in the experimental universe for adult weevils (see Fig. 7). In this instance crowding causes competition for suitable oviposition sites.

Crombie (1942), studying laboratory populations of the beetle *Rhyzopertha dominica* (Fab.) also obtained an intermediate-type curve. He showed that decreasing fecundity with increasing density had two separate causes: competition for oviposition sites and "the interruption of rest and of copulation" resulting from "competition for 'total space' ". Crombie found that copulation greatly increased fecundity and fertility, but that neither fecundity nor fertility were affected by further copulations after the first. Crombie concluded that "any effect density of population may have upon copulation frequency will have no effect upon fecundity and fertility".

Crombie (1943) wrote as follows. "Both Park (1933) and MacLagan (1932) agree that the fecundity of *Tribolium* at densities below the optimum is submaximal because the females have not endured sufficient copulation. Now Park (1933) began his experiments with virgin females. He showed also that copulation in excess of a certain amount had no further effect upon fecundity or fertility. Therefore we should expect that as, with the passage of time, the females came to endure more copulations, fecundity at these low densities would rise to the maximum, and, indeed, an inspection of Park's (1932) data shows that there is a tendency for this to happen. Furthermore, if we began with well-copulated females we should not expect fecundity to be sub-maximal at all at very low densities". Crombie demonstrated experimentally that starting with well-copulated females *Tribolium* could be made to yield a *Drosophila*-type curve. Whether Park and MacLagan's procedure or Crombie's procedure is more meaningful depends on the interests of the reader. If one wishes to test hypotheses about the factors governing dynamics of populations, then Crombie's experiment is the more appropriate; however, my purpose in writing this paper is to develop and present a model for application to *natural* populations. The females in natural populations do not begin adult life conveniently copulated. Hence the situation created experimentally by Park and MacLagan is more typical of the natural insect world than that created by Crombie.

Crombie (1943) also studied the beetle *Oryzaephilus surinamensis* (L.) and obtained an intermediate-type curve for the effect of density on fecundity.

Robertson and Sang (1944) could not duplicate Pearl's (1932) results using *Drosophila*. Under adequate nutritional conditions, they produced an intermediate-type curve. However, they could reproduce Pearl's results when the flies were starving. This paper, like many of the others already reviewed, and a host of papers I have not mentioned, leads us to the conclusion that one of the three types of density-fecundity curves is not peculiar to any insect species, even for a constant range of densities. Rather, which type of curve applies (i.e., what the parameter values for the curve are) in a particular situation depends on a great array of factors extrinsic to the population. After we obtain an equation correctly expressing the effect of density on fecundity, we must then proceed to relate the parameters in the equation to other relevant factors. Where we decide to terminate the process of adding complexity into an equation in any particular instance will depend on the proportion of the total sum of squares in the dependent variable still unaccounted for. In general, this proportion can

be made very small with little increase in the complexity of the equation. Bellman (1957) very aptly describes in his preface the narrow path between over-simplicity and over-complexity the mathematical model-builder must tread. An excessively simple model is unrealistic and useless for mimicking events in the world of scientific measurement and observation; a too complex model is too difficult and costly to handle relative to its conceptual value.

Richards (1947) obtained an "Allee type" curve for experimental populations of *Sitophilus granarius* (L.).

Ishida (1952) found that fecundity decreased with decreasing number of oviposition sites or with increasing population density. By simultaneously varying number of weevils; *Callosobruchus chinensis* (L.) and number of oviposition sites in his experiments, he was able to show that two factors independently depressed fecundity: mutual interference of weevils and availability of oviposition sites. His curves were essentially of the *Drosophila* type.

Using experimental populations of the scolytid, *Blastophagus piniperda* (L.), Nuorteva (1954) obtained an Allee type curve.

Rich (1956) obtained results reminiscent to those of Chapman (1928) and of Park (1932) in that at the first census of his *Tribolium confusum* Duv. populations, he obtained an Allee type curve, but at subsequent censuses, a *Drosophila* curve.

Any realistic mathematical description of the effect of density on fecundity must be in accord with the foregoing facts.

Evaluation of Mathematical Models

We shall now reconsider the six models mentioned in the introduction.

In 1923 Lotka wrote the differential equation

$$\frac{dN_1}{dt} = b_1N_1 - d_1N_1 - a_1N_1N_2, \quad \ldots\ldots(1)$$

where N_1 denotes the number of unattacked hosts,
N_2 denotes the number of adult parasites,
b_1N_1 is the number of hosts born per unit time,
d_1N_1 is the number of host deaths per unit time,
$a_1N_1N_2$ is the number of hosts attacked by parasites per unit time, and
dN_1/dt denotes the rate of change in N_1 with time.

I have already shown that $a_1N_1N_2$ is not a realistic means of expressing the numbers attacked as a function of N_1 and N_2 (Watt, 1959). If it is true that numbers of hosts born per unit time is given by b_1N_1, a graph of b_1 (number of hosts born per unit time per host) against N_1 for any time interval should produce a straight line parallel to the N_1 axis. Patently, from the papers herein reviewed, empirical data yield nothing of the sort. Volterra (1928) makes the same false assumption as Lotka, when he asserts, "If there is only one species, or if the others have no influence on it, so that the circumstances of birth and death do not vary, we shall have, if N denotes the number of individuals,

$$\frac{dN}{dt} = nN - mN = (n - m)\,N,$$

where t denotes time and n and m are constants, respectively the coefficients of birth and mortality". Obviously n is not constant, and once again it is clear that the logistic (which uses the assumption that n is constant) is only a crude generalization, of no use in critical population analysis.

Pearl and Parker (1922) fitted their data to a curve of form

$$\log y = a - bx - c \log x, \quad \ldots\ldots(2)$$

where y denotes imagoes per mated female per day, and x denotes mean density of the mated population (measured as flies per bottle) over the whole 16-day period of the experiment. This equation gave a remarkably good fit to their data, and Pearl was moved to remark, "Plainly the curve is the expression of the law relating these two phenomena – rate of reproduction and density of population". However, equation (2) clearly is not the much-sought-for law, since it does not meet two of the desiderata itemized in the introduction of this paper. First, it yields no insight into the phenomenon, and secondly, it lacks generality. Equation (2) could not account for "Allee type" curves because it has no component producing an increase in log y with increasing x. A really meaningful and general equation has to be capable of yielding Allee-type or *Drosophila*-type curves, since either type can be generated by the same organism, merely by changing, for instance, the time the population has been cohabiting (Fig. 2), density (Kirchner, 1938), degree of copulation (Crombie, 1943), nutritional level (Robertson and Sang, 1944), or any of several other factors, singly or in combination.

Pearl (1932) proposed a new equation to describe *Drosophila*-type curves. Where y denotes eggs per 1,000 female-hours exposure, x represents mean density of population, and c, d and K are constants, he suggested that

$$y - d = \frac{K}{x + c} \qquad (3)$$

This equation suffers from both the limitations of the Pearl and Parker (1922) formula.

Andersen's (1957) fundamental assumption is that above a certain limit of density the fecundity is a linear function of the reciprocal of the density. The best blocks of data available for testing this assumption are those obtained from experiments covering a very wide range of densities. Fig. 8 is a plot of fecundity per female per unit time against the reciprocal of density for two such blocks. The data chosen are from Pearl's (1932) Table 5, representing *Drosophila melanogaster* Meig. in quarter pint bottles, and Utida's (1941c) Table III, *Callosobruchus chinensis* (L.) under 24,8°C. and 74 per cent relative humidity. Andersen's assumption obviously at best only approximates the facts at high densities. However, it yields no insight into the phenomenon we are exploring, and it tells us nothing about the part of the curve for which shape varies most from one case to another. Furthermore it is this part of the curve which should describe the events which are most critical from the standpoint of population survival and growth (i.e. those at low densities). *Drosophila*-type and Intermediate-type curves would appear as the Utida data in Fig. 8 of the present paper. Allee-type curves would appear as the Pearl data in this figure.

Fujita and Utida (1953) proposed a model developed by reasoning from the logistic equation of population growth. According to this model, there should be a rectilinear relationship between the reciprocal of fecundity rate per female, and the population density (where there is no adult mortality during the period when fecundity is assessed). Actually, this relationship only holds for *Drosophila*-type curves. Fig. 9, a plot of Park's data (1932, Table II), illustrates that an Allee-type curve will not be transformed into a straight line by using the Fujita-Utida model. In general, plotting the data from an Allee-type curve as suggested by Fujita and Utida (1953) will produce an asymmetrical "V", not a straight line.

Fujita (1954) subsequently made a more penetrating analysis of the effect of density on fecundity. He recognized the existence of three types of curves

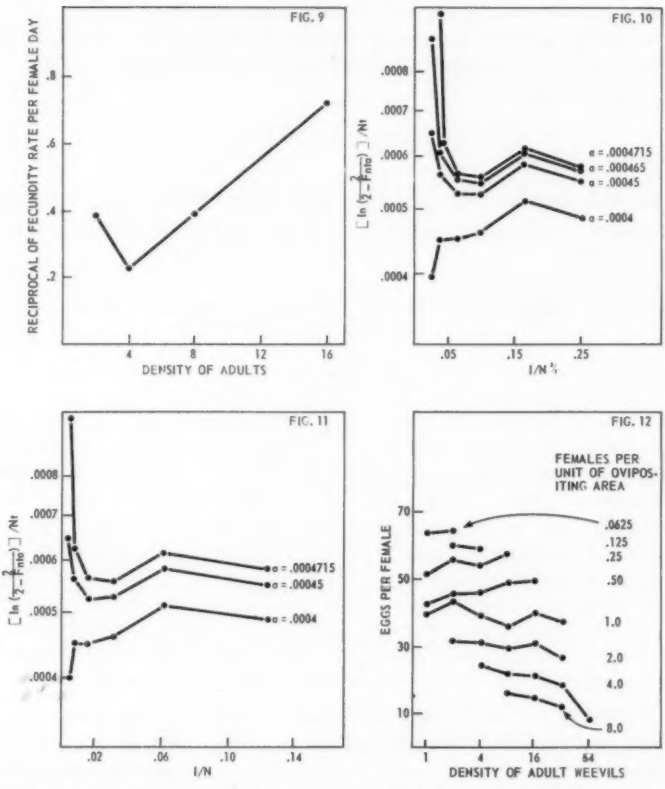


Fig. 9. Test of Fujita and Utida's (1953) equation, using Park's (1932) data.

Fig. 10. Test of Fujita's (1954) model using Rich (1956) data, assuming eggs are laid in volume.

Fig. 11. Test of Fujita's (1954) model using Rich (1956) data, assuming eggs are laid on a plane.

Fig. 12. Separation of the effects of interference and competition for oviposition sites on fecundity. (Data from Ishida, 1952).

(we have been following his classification throughout this paper). However, he made the following important observation: "The type of density effect of a given insect population is not maintained invariable during the course of a particular experiment, but changes systematically as the period of incubation is prolonged". Chapman (1928), Park (1932) and Rich (1956) all obtained data supporting this statement. Hence, Fujita concluded correctly that the density effect was a time-dependent property, and time had to be included in any equation for the effect of density on fecundity.

In the rest of this paper, I shall present the rationale and derivation of the Fujita model, then attempt to fit it to available data. Then after re-examining the logic of his model as critically as possible with the empirical data now available, and showing where the model needs modification, I shall develop and test a new model.

First, certain symbols must be defined

N population density (or population size, if we refer to an enclosed population)

E the total number of eggs laid from time 0 to time t

a the area occupied by a single egg deposited (note that Fujita really means the fraction of the total space available for oviposition which is taken up by 1 egg, so that when $E = 1/a$,

$$1 - aE = 1 - \frac{a}{a} = (0.)$$

ϵ the intrinsic rate of oviposition for a given environmental condition

P the frequency of copulation per female (the number of copulations per female per unit time)

k a proportionality constant

Fujita then writes

$$\frac{dE}{dt} = k \epsilon NP (1 - aE) \quad \ldots\ldots (4)$$

Equation (4) is eminently reasonable. However, many writers, including Crombie (1943), MacLagan and Dunn (1935), Park (1936), Richards (1947), Robertson and Sang (1944) and Utida (1941b) have shown that environmental factors govern ϵ. Park (1936) showed experimentally that one could obtain curves relating ϵ to an index of an environmental parameter. Stanley (1934) worked out a mathematical model by which the decline in fecundity as a function of environmental condition could be predicted, if one had all necessary measurements of the environment. However, there are not enough data available now to work out a Stanley-type equation for a natural population, so Fujita contented himself with detailed study only of P, hoping by so doing that he could produce a version of (4) that would be useful as a first approximation.

Fujita makes the following assumptions.

(1) Copulation frequency is increased by increasing adult density. Further, "if the collisions are made entirely in a random fashion, it may be assumed that P is represented by a Gaussian distribution function with respect to the average mutual distance between neighbouring adults, r. Namely, we may put

$$P = \exp(-\sigma r^2),$$

where σ is a constant dependent primarily on the copulation characteristics of the given insect species".

(2) Fujita assumes that in a two-dimensional universe,

$$N \sigma r^2 = \alpha,$$

$$\text{or} \qquad \sigma r^2 = \alpha / N$$

Hence

$$P = \exp(-\alpha / N) \quad \ldots\ldots (5)$$

(3) A hidden assumption is contained in equation (4). We know that oviposition rate is some function of copulation frequency, which in turn is some function of density. In symbolic terms, we could write

$$\frac{dE}{dt} = f_1 (P) = f_2 (N).$$

Fujita devotes considerable attention to the form of function f_2, but immediately assumes that $dE/dt = f_1 (P)$ is a simple rectilinear relationship. I know of no data which will support this assumption.

Inserting (5) into (4) we get.

$$\frac{dE}{dt} = k \epsilon \exp(-\alpha/N) N (1 - aE)$$

$$\text{or } \frac{-\ln(1 - aE)}{a} = k \epsilon \exp(-\alpha/N) Nt$$

$$\text{or } 1 - aE = \exp(-ak \epsilon e^{-\alpha/N} Nt)$$

$$\text{or } E = \frac{1}{a}\left\{1 - \exp(-ak \epsilon e^{-\alpha/N} Nt)\right\}$$

But since, assuming a sex ratio of 50:50, the mean fecundity, F, per female per unit time is

$$F = \frac{E}{1/2\ Nt} = \frac{2E}{Nt},$$

therefore

$$F = \frac{2}{Nta}\left\{1 - \exp(-ak \epsilon e^{-\alpha/N} Nt)\right\} \quad \ldots\ldots(6)$$

Fujita's assumption (1) is suspect immediately in view of some of the findings we reviewed, as Fujita himself conceded: for example Figs. 3 and 6 both have descending limbs as density increases. However, for the moment let us confine our attention only to assumption (2).

If oviposition can occur in a volume rather than a plane, then

$$N \sigma r^3 = \alpha \quad \ldots\ldots(7)$$

This merely states that number of adults x volume/adult = total volume. It is true for a volume, as for a plane, that the probability distribution function for chances of contact is

$$P = \exp(-\sigma r^2) \quad \ldots\ldots(8)$$

But from (7),

$$\sigma r^2 = \sigma^{1/3}\left(\frac{\alpha}{N}\right)^{2/3}, \quad \text{or}$$

introducing a new constant,

$$\sigma r^2 = \left(\frac{\beta}{N}\right)^{2/3} \quad \ldots\ldots(9)$$

Inserting (9) in (8),

$$P = \exp\left\{-\left(\frac{\beta}{N}\right)^{2/3}\right\} \quad \ldots\ldots(10)$$

And substituting for P in (4),

$$\frac{dE}{dt} = k \epsilon N \exp\left\{-\left(\frac{\beta}{N}\right)^{2/3}\right\}(1 - aE) \quad \ldots\ldots(11)$$

and proceeding as in the deviation of (6), we obtain

$$F = \frac{2}{Nta}\left\{1 - \exp(-ak \epsilon e^{-(\beta/N)^{2/3}} Nt)\right\} \quad \ldots\ldots(12)$$

A simple procedure for testing the validity of equations (6) and (12) may be worked out as follows.

From equation (6),

$$1 - \frac{FNta}{2} = \exp(-ak\epsilon e^{-(\alpha/N)}Nt),$$

$$\ln\left(\frac{2}{2 - FNta}\right) = a\,k\,\epsilon\, e^{-(\alpha/N)}Nt,$$

$$\ln\left[\frac{\ln\left(\frac{2}{2 - FNta}\right)}{Nt}\right] = \gamma - \alpha/N \quad \ldots\ldots(13)$$

And similarly, where oviposition sites are in a volume,

$$\ln\left[\frac{\ln\left(\frac{2}{2 - FNta}\right)}{Nt}\right] = \gamma - (\beta/N)^{2/3} \quad \ldots\ldots(14)$$

Since in some cases it may not be clear exactly how the adult females search for oviposition sites, in order to make a really thorough test of Fujita's model we should attempt to fit both equation (13) and (14) in these instances.

The best fit we can obtain for (13) or (14) is found by selecting (by trial and error), that value of a which minimizes the residual sum of squares from the regression of the transformation

$$\ln\left[\frac{\ln\left(\frac{2}{2 - FNta}\right)}{Nt}\right] \text{ on } 1/N \text{ or } 1/N^{2/3}.$$

We can find out quickly which fine range of values for a we should be exploring by plotting

$$\left[\frac{\ln\left(\frac{2}{2 - FNta}\right)}{Nt}\right] \text{ against } 1/N \text{ or } 1/N^{2/3}$$

on semi-log graph paper. The process is illustrated in Figs. 10 and 11, using Rich's (1956) 8-hour data.

It is clear from these graphs that Fujita's equation can not be used to produce a straight-line plot using Rich's data; hence we must reconsider Fujita's assumptions.

Re-examining Fujita's basic equations

$$\frac{dE}{dt} = k\,NP\,(1 - aE),$$

we find that this allows for one factor (copulation and recopulation) which stimulates fecundity with increasing density, and one (competition for oviposition sites) which decreases fecundity with increasing density. There is sound empirical support for the assumption that both copulation (but not recopulation) and competition for oviposition sites operate. Park (1933) and Crombie (1942, 1943) clearly demonstrated the fecundity-elevating effect of copulation; Utida (1941d), Crombie (1942) and Ishida (1952) proved the existence of competition for oviposition sites.

However, there is a group of density-dependent factors, apart from competition for oviposition sites, which can depress fecundity and which Fujita has not taken into account. For example, Smirnov and Wiolovitsh (1934) and Smirnov and Polejaeff (1934) showed that sterility of females increases with increasing population density. Also, Crombie (1942) showed that increasing the density of males can decrease the total number of copulations by causing increased fighting. Some clarification of the difference between mode of operation of competition for oviposition sites and other types of interference seems necessary at this point. If N adults live in a very large area which includes only a small area suitable for oviposition there will be no sterility or failure to copulate due to interference. However, fecundity may be low due to competition for oviposition sites. If, on the other hand, N adults live in a small area, most of which is suitable for oviposition, there will be appreciable depression of fecundity due to interference-induced phenomena but not much due to competition for available oviposition sites.

Experiments have been performed which clearly demonstrate, by manipulating oviposition area and total area independently, that phenomena other than competition for oviposition sites can depress fecundity. For example, Robertson and Sang (1944) varied the oviposition area available to 10 pairs of *Drosophila* in bottles. A seven-fold decrease in density of adult *Drosophila* per unit of available oviposition area produced only an 11 per cent increase in the fecundity per female per day. Robertson and Sang concluded that Pearl's (1932) results could not be explained on the basis of competition for oviposition sites alone. Rather, some other effect which depresses fecundity with increasing densities must be postulated to account for the observed magnitude of Pearl's fecundity-depression. Also, Ito (1955) showed that fecundity of flour beetles, *Tribolium castaneum* (Hbst.) decreased if there was no air space above the flour in the container. Now if all other variables are held constant, but removing an air space depresses fecundity, this depression must be caused by increasing density-dependent competition of some type other than competition for oviposition sites. Ishida (1952) performed an experiment in which number of available oviposition sites per female and volume of the universe per female were the two independent variables in a factorial design. The results of his experiment for oviposition sites, as measured by females per unit oviposition area, is held constant, there is some other component of competition which can depress the fecundity as density increases (see the 4 females per unit oviposition area line, for example).

A new model is clearly needed to incorporate these factors. The model will be expressed, first, as three partial differential equations which describe the operation of each of the three components of the density-fecundity mechanism. Then the three partial differential equations will be combined to yield one integral equation.

First, we can write

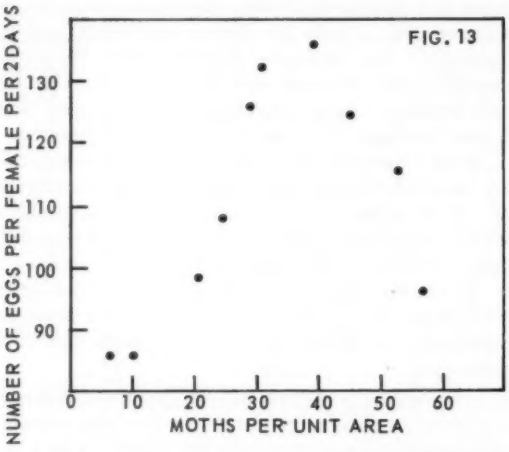
$$\frac{\partial E}{\partial t} = k \epsilon NPI (1 - aE) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (15)$$

This states that, all other factors being held constant, the rate of change of density of eggs with time, $\partial E/\partial t$, is equal to the product of the following six components.

k a proportionality constant

ϵ the intrinsic rate of oviposition for a given environmental condition

N population density



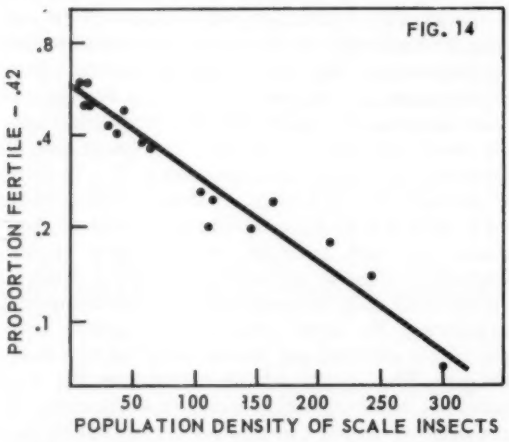


Fig. 13. The effect of moth density on rate of reproduction in *Anagasta kühniella* Zell. (Data from Ullyett, 1945).

Fig. 14. Test of equation (17) using data of Smirnov and Wiolovitsh (1934) on natural populations of *Chionaspis salicis* L.

P the effect of probability of contact on fecundity (note that P is being defined differently than it was by Fujita. Also, following Crombie (1942), we concede that no contact after the first need be important).

I the effect of interference on fecundity

1-aE the effect of competition for oviposition sites on fecundity, where a is defined as by Fujita.

Secondly, we need to determine the form of the relation between P and N. The best data for this purpose are those for rather low population densities. Examining the data of Utida (1941d) in Fig. 6, and Ullyett (1945) in Fig. 13, for example, we are led to the conclusion that P and N are related by

$$\frac{\partial P}{\partial N} = b\,P\,(1 - P), \qquad (16)$$

where b is a constant. The ascending limb of Ullyett's curve was well described by the logistic equation.

Thirdly, it is necessary to know how N governs I. We can obtain a general expression for I by analyzing data from studies wherein the effect of N on I was measured separately. Smirnov and Polejaeff (1934) and Smirnov and Wiolovitsh (1934) measured the effect of population density on female sterility in two species of scale insects on lime and ash trees in Moscow parks and squares. Where I_{min} represents the minimum level to which I can be driven by increasing density, analysis of the data by Smirnov and associates shows the relation

$$\frac{\partial I}{\partial N} = - f (I - I_{min}),$$

where f is a constant, or

$$\ln (I - I_{mm}) = d - fN. \quad \ldots\ldots (17)$$

This relation is illustrated in Fig. 14, for the Smirnov and Wiolovitsh (1934, Table II) data.

It is reasonable to assume that population density can decrease fecundity via other interference phenomena in the same way as it affects fecundity via sterility. Assuming that (17) is a general equation for the effect of population density on fecundity, operating through interference, will explain various observations discussed hitherto in this paper. It accounts for the descending limbs of the curves in Figs. 3, 6 and 12, none of which can be explained by competition for oviposition sites.

Integrating (15) we get

$$E = \frac{1}{a}\left[1 - \exp(-a k \epsilon N P I t)\right] \quad \ldots\ldots (18)$$

With a 50:50 sex ratio the mean fecundity, as before, will be

$$F = \frac{2E}{Nt} = \frac{2}{aNt}\left[1 - \exp(-a k \epsilon N P I t)\right] \quad \ldots\ldots (19)$$

From (16) and (17), respectively, we find that P and I are given by

$$P = \frac{1}{1 + e^{C-bN}}$$

$$I = I_{min} + e^{d-fN}$$

and substituting these into (19), we obtain

$$F = \frac{2}{aNt}\left\{1 - \exp\left[-ak\epsilon N\left(\frac{I_{min} + e^{d-fN}}{1 + e^{C-bN}}\right)t\right]\right\} \quad \ldots\ldots (20)$$

The effects of changes in the various parameters on shape of (20) are illustrated by Figs. 15, 16, 17 and 18. Additional insight into behavior of functions such as (20) may be gained from study of Fujita's (1954) Figs. 4 and 5.

One more constant may be required to fit data with (20). Sometimes, as in Ullyett's (1945) data, the locus of F intercepts the F-axis not at zero, but at some value A.

There was no point in testing (20) against Rich's (1954) data, since the number of parameters in (20) exceeds the number of pairs of values Rich collected at any one time. However, (20) has been fitted to an observed Allee-type curve (Table I) with 10 points, and an observed *Drosophila*-type curve (Table II) with 14 points.

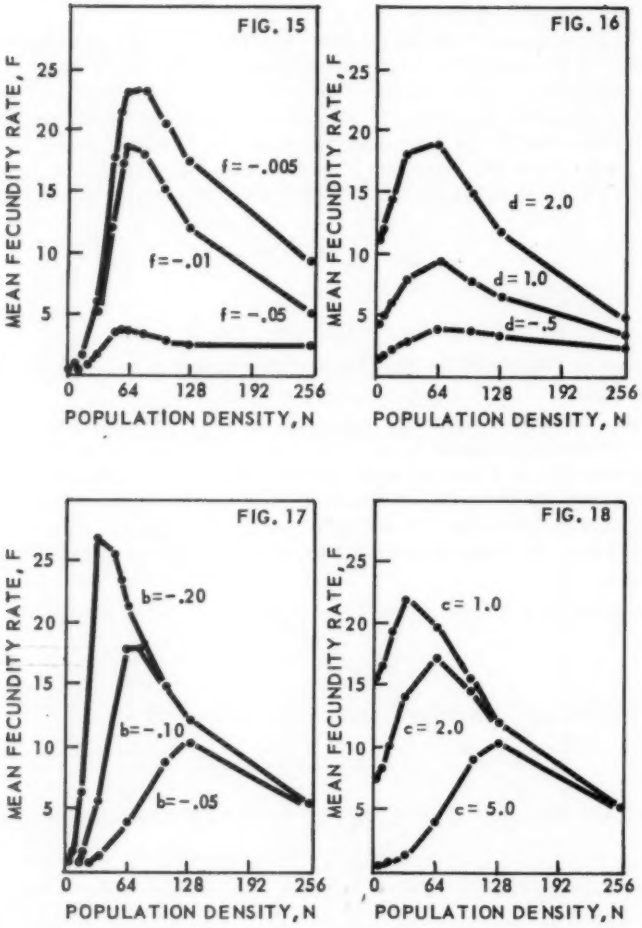


Fig. 15. Behavior of function (20). Smaller negative f values reflect decreased effect of population density on interference. Other values used were t = 1, a = .0006, a k $_{\epsilon}$ = .002, c = 5.0, b = −.10, d = 2.0 and I_{min} = .4.

Fig. 16. Behavior of function (20). Decreasing d values shows effect of decreasing minimum level of interference. Other values used were t = 1, a = .0006, a k $_{\epsilon}$ = .002, c = 1.5, b = −.05, I_{min} = .4 and f = −.01.

Fig. 17. Behavior of function (20). Decreasing b values indicate increasing effect of probability of contact on fecundity. (The greater b is, the less fecundity is stimulated by increasing population densities). Other values used were t = 1, a = .0006, a k $_{\epsilon}$ = .002, c = 5.0, d = 2.0, f = −.01 and I_{min} = .4.

Fig. 18. Behavior of function (20). Increasing c values reflect decreasing minimum fecundity rate. That is, the lower c is, the higher the fecundity rate will be at N = 2. Other values used were t = 1, a = .0006, a k $_{\epsilon}$ = .002, d = 2.0, f = − 0.1, b = −.05 and I_{min} = .4.

TABLE I
Simulation of data on oviposition by *Anagasta kühniella* (Zell.) (from Ullyett, 1945) using equation 20

Moths per cage	Observed number of eggs per female	Calculated number of eggs
6	86	87
10	86	88
20	99	97
24	108	108
28	126	126
30	132	134
38	136	135
44	125	128
52	116	118
56	96	96

Parameter values (days): t = 2.;, a = .00054, a k ϵ = .0020, c = 31.8, b = −.70, d = 28.1, f = .493, $I_{min.}$ = 0.0, A = 86.0.

It will be noticed that a k ϵ is equal to .0020 in both tables. In fitting the curves, a k ϵ was deliberately held constant to make the point that these symbols in (20) are redundant. That is, the shape of the curve is completely defined by the other parameters. There is no such thing as "an intrinsic rate of oviposition for a given environmental condition", as this quantity is density-dependent. Hence, the correct form of (20) is

$$F = A + \frac{2}{aNt}\left\{1 - \exp\left[-aNt\left(\frac{I_{min} + e^{d-fN}}{1 + e^{c-bN}}\right)\right]\right\}$$

Discussion

An immediate implication of (20) is that if insects are being mass-reared in the laboratory, there is a density for any cage size at which NF will be a maximum. It is economically worthwhile to ascertain this maximum.

TABLE II
Simulation of data on oviposition by *Callosobruchus chinensis* (L.) (from Utida, 1941 c), using equation 20

Population density	Mean oviposition rate per female under 30.4°C and 76% R.H.	
	Observed	Calculated
2	88.7	86.0
4	81.0	83.3
8	70.7	78.6
16	57.4	69.3
32	50.1	56.1
48	51.0	47.4
64	47.8	42.1
96	46.9	36.1
128	38.4	33.5
192	38.7	31.9
256	31.9	31.4
384	28.7	30.5
512	29.4	29.6
768	16.8	27.4

Parameter values: t = 1.0 (assumed, since t not given by Utida), a = .000035, a k ϵ = .0020, c = −1.8, b = −.01, d = −.5, f = −.027, $I_{min.}$ = .30, A = 0.0.

Extensions of previous research on insect fecundity would produce data useful in checking, modifying, and making practical application of equation (20).

Experiments are needed covering a wide range of population levels, including very low densities, to aid in interpretation of events in the field at endemic levels. Also, experiments covering a large number of different densities are necessary because one degree of freedom is lost for testing an equation for each extra parameter used in the equation. Most realistic mathematical models of population phenomena require six or more parameters. It would therefore be desirable to have data on 20 or more different densities, with, say, 10 replicates or more at each density.

More experiments are needed to check the form of equations (16) and (17). Analytical experiments such as those of Ishida (1952), Park (1933) and Utida (1941d) are required to separate the effects of interference and competition for oviposition sites. It is becoming apparent that the most immediate consequence of mathematical population analysis is to show that more analytical experiments on behavior are required to produce data of the type collected by Smirnov and associates. It would be useful to know the effect of density on each component of interference separately. Not nearly enough data are available revealing the effect of density on natural populations.

An extremely important gap in our knowledge that should be filled quickly concerns the effect of very low densities on mating behavior. Figs. 6 and 13 suggest that fecundity rate may not rise much above its minimum value until a certain threshold population density has been surpassed.

In spite of these deficiencies in our knowledge, enough is known to draw some conclusions that have implications for insect pest control.

First, equation (20) implies that a reduction in population density N may not in fact reduce the total number of eggs produced by the population. As shown in Figs. 15 to 18, some populations have characteristics such that a considerable decrease in N may result in an actual increase in the size of the progeny generation. Where the fecundity curve is of an extremely steep *Drosophila*-type, decreasing N might result in a subsequent large population increase. (Populations have many built-in homeostatic mechanisms to ensure their survival.) The point has two implications for pest control. First, if short-term screening of control methods and agents is employed, we may be getting very misleading comparisons. The poorest control measure from a long-term standpoint (e.g. certain insecticides) may have a catastrophic short-term effect on a pest population, but may elicit a large-scale homeostatic reaction on the part of a population. On the other hand, a control method that is by no means spectacular in its initial effort may be best from a long-term point of view, because it gradually erodes the pest population's homeostatic capability. Hence a truly objective comparison of control methods can only be made over more than one generation.

Secondly, in general, all other things being equal, an Allee-type fecundity curve renders a population more vulnerable to extinction at low densities, and hence more subject to control by any means than a *Drosophila*-type curve. Therefore, any genetic mechanism which could be exploited to convert a pest population from *Drosophila*-type to Allee-type could be of economic importance. Furthermore, a laboratory-produced *Drosophila*-type strain could be used to quickly spread deleterious alleles through a natural Allee-type pest population at endemic periods of a long-term sequence.

Rather more complex implications of (20) appear when we consider the interaction of chemical and biological control agents. Our points can perhaps be made most mnenonical by means of a hypothetical situation.

Consider a *Drosophila*-type pest population that is controlled in nature by two entomophagous insects, A, an Allee-type insect, and D, a *Drosophila*-type insect. Now it is a basic tenet of modern ecological thinking that there will be lower masses, and hence densities, for large species, of A and D than the pest in any natural community. This is because of the low thermodynamic conversion efficiency from one level of a food pyramid to the next higher level, and in the case of a predator may also be because of the greater linear dimensions of the predator (Hutchinson, 1959). Now suppose the populations of the pest, of A, and of D are all reduced x per cent by a non-species-selective insecticide. Clearly, A will have had its position made relatively worse than that of the pest, because of the great difficulty individuals of A will have in finding mates at very low densities. If A were the only entomophagous insect present, an insecticide could clearly help the pest in two ways. The pest's fecundity rate would shoot up, and density level and improbability of extinction relative to that of A would be raised.

Clearly, such ecological mechanisms, together with physiological and genetic mechanisms already well known, can help explain why insecticides may not annihilate a pest after repeated application.

On the other hand, D does not have its long-term position relative to the pest made as tenuous as that of A. An implication is that if we want to use a combination of chemical and biological control agents, D type entomophagous insects will fare better than A type.

To gain deep insight into the mechanics of pest control, we need means of handling very large mathematical models of pest population dynamics containing terms for all relevant factors. Otherwise the significance of interactions of terms such as (20) and attack models (Watt, 1959) and terms for weather, stand factors, etc. will not be apparent. Accordingly, such means will be outlined in another paper.

Summary

Data on the effect of population density on fecundity in insects are discussed and used to test various mathematical models. A new model is developed in the light of available data; its behavior is illustrated and fits to examples of two types of cases are given. Implications of the model for insect pest control are suggested, and areas where more work is needed are pointed out.

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A Laboratory Method for Rearing Predators of the Balsam Woolly Aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae)[1, 2]

By R. C. Clark[3] and N. R. Brown[4]

In a previous paper (Clark and Brown, 1959) a field cage was described for rearing syrphid larvae and other predators of the balsam woolly aphid. The cages proved satisfactory in the field but some method was necessary to supplement the results with data for individual predators reared in the laboratory under controlled conditions.

In the past, attempts to rear predator larvae in the laboratory on small pieces of infested bark proved unsatisfactory because of the difficulties of keeping the bark moist and suitable for prey development and preventing the growth of moulds on the prey, the bark, and the containers. In most cases when small petri dishes or other containers were used the prey or predators died before rearing was complete or the individuals which survived were unhealthy and not representative of normal prey or predator development.

To overcome these difficulties a method was developed whereby a continuous flow of moist air was passed through a series of glass jars set up in this case in a laboratory fume cabinet adapted for the purpose (Fig. 1). This prevented or retarded the growth of moulds and the drying out of the bark and prey, and provided a suitable environment for rearing of predator and prey.

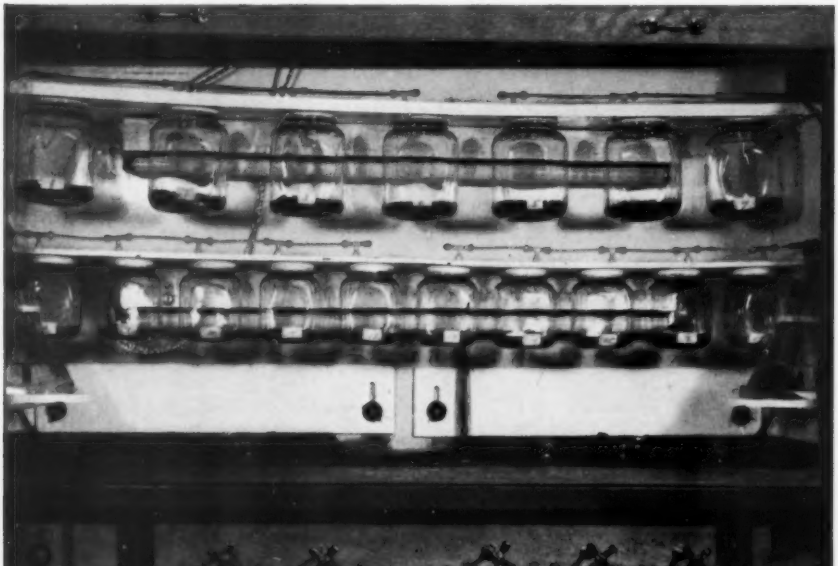

Fig. 1. Battery of rearing jars supplied with a continuous flow of moist air and used for rearing predators.

[1]Contribution No. 636, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

[2]Part of a joint project of Forest Biology Division, Fredericton, N.B. and Department of Lands and Mines of New Brunswick, financed in part by funds from the Provincial Department.

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The containers used were wide-mouthed glass jars of one gallon or one-half gallon capacity with screw type metal lids. The wide mouths facilitated the insertion or removal of material. The lids were securely fastened to a ½-inch plywood shelf and two ¼-inch holes were drilled through the plywood and each lid. One-quarter-inch polyethylene tubing and polyethylene T-type connectors were used to connect one of the ¼-inch openings in each jar with the main air supply. A short piece of tubing was inserted into each of the remaining holes and these served as air outlets (Fig. 1). A one-inch layer of vermiculite partially covered by a sheet of ordinary blotting paper was placed in the bottom of each jar. This helped to maintain high humidity in the jars and the vermiculite also served as a pupation site for those predators which pupate in the soil in nature.

The air from the main supply was passed first through a large flask of distilled water (by means of a length of perforated polyethylene tubing) and then allowed to flow continuously through each of the jars. After regulating the main air supply and adjusting the size of the inlet tubes, the moist air circulated in each of the jars at approximately the same rate. The temperature within the jars without using any special heating or cooling devices usually varied between 70° and 80°F., depending on room temperature, and the relative humidity was about 100 per cent.

To facilitate observations of the predators and prey, fluorescent tubes were installed behind each series of jars. These lights remained on approximately eight to ten hours each day when rearing was in progress; their effect on the temperature within the jars was negligible.

By using this simple method we have managed to rear successfully several predator species which were difficult if not impossible to rear in the past.

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Clark, R. C., and N. R. Brown. 1959. A field cage for rearing syrphid larvae and other predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). *Canadian Ent.* 91(11): 723-725.

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Another Holarctic Species of Tabanidae (Diptera)

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The species of the genus *Hybomitra* (*Tylostypia*) have been most vigorous of the family Tabanidae in colonizing the boreal regions. However, the number of holarctic Tabanidae of this genus is surprisingly few in consideration of the 53 species assigned to North America and the 86 to Eurasia. Only *H. sexfasciata* (Hine; *borealis* "Lw." of authors), *H. aequetincta* (Becker) and *H. epistates* (O.S.) in addition to *Chrysops nigripes* Zett. have crossed the northern Atlantic and/or Pacific Oceans (Philip, 1956). It is not surprising therefore to discover that there is an additional holarctic species which has been known under two different names in the Old and New Worlds.

Hybomitra arpadi (Szilady)

Tabanus (*Therioplectes*) *arpadi* Szilady, 1923, Biologica Hung. *1*: 7; ♀, Lapland, Amur (published mailing date, 10 June 1923); types recorded as in

Hofmuseum in Vienna may still be in existence. Kröber (1939) gives *T. morgani* Surcouf, 1912, as a questioned prior name, but the locality, Persia, makes this synonymy very doubtful.

Olsufjev (1937) redescribes and refigures ♀ in subgenus *Tylostypia*, adds ♂, and compares to *H. fulvicornis* (Meigen) from which the above is distinguished in the female by darker, more slender antennae, sharper dorsal angle of the plate and narrower, differently-structured callosity; and in the male, by dark pile on the eyes and erect, black-hair patches on the second to fourth abdominal tergites.

The distribution of *H. arpadi* is given as the taiga from Leningrad to Kamchatka, north to Murmansk, and south to Altai Range in the west and lower Amur in the Far East; Finland.

Through courtesy of A. Lutta, I received a pair and two females collected by her in Karelia, the pair collected on same date in Kifau Kondopozhsk, 10. vii. 1956. These prove not to be separable from *H. gracilipalpis* (Hine), both sexes of which are available for comparison.

Syn. *Tabanus gracilipalpis* Hine, 1923, Canad. Ent., *55*: 143; ♀, Alaska (published mailing date, 25 June 1923). Stone, 1938, U.S.D.A. Misc. Publ. No. 305, p. 132 (synonymy). Philip, 1941, Canad. Ent., *73*: 150 (*Hybomitra*); 1947, Amer. Mid. Nat., *37*: 294 (references and synonymy).

Syn. *Tabanus cristatus* Curran, 1927, Canad. Ent., *59*: 81; ♂, Alberta, ♀ allotype from Labrador. Philip, 1937, Canad. Ent., *69*: 37.

Considering the wide difference in localities, it is remarkable that Curran (op.cit.) was able correctly to associate the sexes, which remained in doubt by both Philip and Stone (op.cit.), but has since been confirmed by a pair on the same pin (presumably in copula) in the Canadian National Collection from Manitoba. Though the females are separated with difficulty from the more ubiquitous *H. affinis* (Kirby) (Philip, 1937, Miller, 1951), it may be significant that the latter is not identifiable with certainty in the Siberian fauna; a species misidentified as *H. arpadi* by Philip (1956) from Manchukuo is certainly close and may be the same if differences in the eye pattern, and still unknown male, are eventually reconciled with the Nearctic *H. affinis* ♂ ♀. It is difficult to understand why so ubiquitous a Nearctic boreal species would not have transgressed the geologically recent Bering land bridges between the two continents. *H. affinis* has been one of the most vigorous colonizers of boreal North America and constitutes one of the worst pests of warm-blooded animals throughout Canada and the northern U.S.A.

The above synonymy is based upon comparison of the Karelia specimens with: homotypes compared with the holotypes of *T. gracilipalpis* Hine (USNM; a ♀ det. Hine from Tom's Village, Naknek Lake, Alaska, July 1919, coll. J. S. Hine), of *T. cristatus* Curran (Canad. Nat. Coll.; a paratype ♂ from Nordegg, Alberta, 11.vii.1921, McDunnough), and with the Naknek ♀ (compared with Labrador allotype ♀, Canad. Nat. Coll.).

Specimens of syn. *H. gracilipalpis* have been examined as follows: males, Nordegg, Alta., Eagle Pass, Alaska, and Cedar Lake, Man.; females, Alaska, Alta., Man., Minn., Wisc., Mich., N.B., and Labr. Specimens are recorded from the northern counties of Michigan (Hays, 1956), Wisconsin (Roberts and Dicke, 1958), Minnesota (Philip, 1931); and from the northern (Churchill) area of Manitoba (Twinn *et al*, 1948, and Miller, 1951, reared). A female from Gulkona, Alas., 21.vii.1937, C. B. Philip, off horse, has predominantly red-haired, hind tibial fringe analogous to some New England *H. aurilimba* (Stone) females. A

female from Cape St. Charles, Labr., 11.vii (no year) agrees with allotype ♀ of syn. *T. cristatus*.

With the exception of Norway and Sweden, *H. arpadi* is recorded across northern Eurasia and entirely across northern North America. At least in the Nearctic Region in spite of this wide distribution, prevalence does not compare with other more common species of *Hybomitra*, such as related *H. affinis*.

It is a coincidence that Szilady's and Hine's species were described in publications mailed on two different continents within 15 days of one another. Though the first page of Szilady's fascicle states "emissum die 15.iii.1923," the date, June 10, 1923, is printed on the cover. The number of Canadian Entomologist in which Hine's description occurs terminates with the statement "mailed June 25th, 1923." These dates were corroborated for me by Professor Aradi Mátayás Pál of Central Institute of Hygiene, Budapest, and Drs. Alan Stone of the U.S. National Museum, J. F. McAlpine of Entomology Research Institute, Ottawa, and L. L. Pechuman, Lockport, New York.

Summary

The name *Hybomitra arpadi* (Szilady), as applied to an Eurasian species, is shown to antedate *H. gracilipalpis* (Hine) from North America. This provides another of the few known holarctic species of Tabanidae.

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Relation of Body Weight to Fecundity in Queen Honeybees

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Introduction

In a recent communication, Hoopingarner and Farrar (1959) report that the weight of the queen honeybee is genetically controlled, and that a proportional relationship exists between body weight and the number of ovarian tubules. These statements corroborate the findings by Eckert (1934) who found that the number of ovarioles tends to be influenced by hereditary factors. In a subsequent study Eckert (1937) was unable to correlate number of ovarioles with actual brood production. Whether a queen with a greater body weight is capable of laying more eggs than a small and lightweight queen remained to be determined; hence the present study was undertaken.

Materials and Methods

Sixty-three queens were removed on August 15, 1956, from colonies that had been established from two-pound packages installed the previous spring. All queens and bees were obtained from the same breeder. Immediately after removal, the queens were gassed with Cyanogas and weighed at once on an analytical balance. Exactly ten days later, the colonies from which the queens had been removed were gassed and the brood combs photographed; at the same time, all adult bees of each hive were weighed. The amount of sealed brood in each colony was determined from the photographs by counting all capped cells and converting to brood area.

Results

The following three variables were considered in this experiment:
X_1 = weight of the queen (milligrams);
X_2 = weight of adult bees in each colony (ounces);
Y = area of sealed brood in each colony (sq. inches).
A multiple regression equation for Y on X_1, and X_2 was determined, and it was found that, under the conditions of this experiment, only the regression of area of sealed brood on weight of queen was significant ($p < 0.01$), and the equation was found to be

$$Y = \overline{Y} + b_{y} (X - \overline{X})$$
$$= 461.3 + 1.57 (X - 272.2)$$

Table I
Analysis of Variance for testing Multiple Regression of brood area (Y) on weight of queen (X_1), and weight of adult bees (X_2).

	SS	d.f.	MS	F
Total	314,817	62		
Regression	80,521	2	40,261	10.31**
Deviation	234,296	60	3,905	
Regression on X_1 (ignoring X_2)	72,239	1		18.5***
Regression on X_2 (eliminating X_1)	8,282	1		2.1
Regression on X_2 (ignoring X_1)	13,142	1		3.4
Regression on X_1 (eliminating X_2)	67,379	1		17.3***

[1]Former Chief, Apiculture Division, Experimental Farms Service, Canada Department of Agriculture, now deceased.

Discussion

The experiment was undertaken to determine to what degree body weight of the queen and/or number of adult bees in the hive provide an index to the amount of brood raised by a honeybee colony. From the results it appeared that the area of the brood nest was influenced by the queen's body weight, but not by the total adult bee population. The correlation coefficient $r = 0.479^{**}$ indicated that about 23 per cent of the total variation in the size of the brood area could be attributed to the body weight of the queen. The rest of the variation could not be accounted for in this experiment.

However, it is not anticipated that body weight would be the only index to the reproductive capacity of queen honeybees; nor is it claimed that this relationship would be the same under different environmental conditions or with other stocks. Further work is necessary to determine the extent to which these and other factors alter the relationship between the queen's body weight and her brood production.

Summary

The fecundity of 63 queens was determined. Weight of queen was found to be significantly correlated with brood area. Total adult bee population was not related to weight of queen or brood area.

Acknowledgments

The authors gratefully acknowledge the assistance of Mr. J. E. Sherman in handling the experimental colonies; appreciation is expressed for advice received from the late Mr. C. Reimer, Statistical Research Service, Canada Dept. of Agriculture.

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Resistance to Low Temperatures of the Overwintering Stages of Two Introduced Parasites of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae)

By J. A. JUILLET[1]

Two introduced hymenopterous parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), are established and widely distributed in southern Ontario: the braconid *Orgilus obscurator* (Nees) and the ichneumonid *Temelucha interruptor* (Grav.). Though these two species are economically important in the control of the shoot moth in Europe, they have never become efficient in Canada. A possible cause of their lack of efficiency may be their susceptibility to low temperatures.

This paper is a report on an investigation of the ability of these parasites to withstand low winter temperatures. Laboratory experiments were conducted to determine the resistance of the overwintering larval stages of the parasites to low temperatures. Field observations on the mortality of host and parasites were

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made at the Waterloo County Reforestation Area, Elmira, near Guelph, Ontario, during the winter of 1958-1959.

Materials and Methods

For the laboratory studies, infested red-pine buds were collected near Elmira in late October, 1958, and stored at −9°C. until needed. Samples each of 50 infested buds were placed in wooden boxes and exposed for various periods of time to various temperatures (Table I). The wooden boxes slowed the rate of change from the storage to the treatment temperature; this cooling period lasted approximately three hours. After exposure to low temperature, the infested buds were brought back to the original storage temperature, and then gradually to room temperature (about 22°C.) over two to four days when the buds were broken open for the dissection of the host larvae.

For the field studies, successive collections of infested buds were made throughout the winter of 1958-1959 to supplement the laboratory findings. These were placed in a cold room as soon as possible and gradually brought back to room temperature for immediate dissection. The minimum temperature recorded between each period of collection was obtained from data recorded at the Ontario Agricultural College, Guelph.

In the early spring of 1959, additional collections of 100 host larvae in each of three two-foot zones above the ground were made to analyse the overall effect of low temperature and snow on the survival of the parasites. The host larvae were dissected immediately.

Results

Whether the host was parasitized or not had no apparent effect on its mortality caused by low temperatures (Tables I to III). This was expected because the parasites had done so little feeding in the overwintering host larvae that the latter were virtually unharmed.

O. obscurator was as resistant to low temperatures as its host, *R. buoliana*, as all parasite larvae were alive in the living host larvae (Tables I to III). *T. interruptor* was slightly less resistant to low temperatures than its host (Tables I and II).

Snow covered the plantation to a depth of two feet throughout January and February, when the temperature was as low as −26°C. This layer of snow afforded protection to the shoot moth larvae up to three feet above the ground (Table III), as many branches of the middle zone were bent down by the weight of snow on the foliage.

Parasitism by *O. obscurator* was approximately the same at all three crown levels (Table III). This means that the *O. obscurator* population remains relatively unchanged with regard to the host population as no difference in host mortality due to low temperatures was observed between parasitized and non-parasitized host larvae. *T. interruptor* was more prevalent at the upper crown levels where winter mortality of the host was more severe. This indicates that the *T. interruptor* population surviving the winter is less in relation to the surviving host population than it was on the previous autumn, as *T. interruptor* is less resistant to cold than is its host, *R. buoliana*.

Summary

The parasites *Orgilus obscurator* (Nees) and *Temelucha interruptor* (Grav.) are able to withstand the low winter temperatures to which their host, *Rhyacionia buoliana* (Schiff.), is exposed. However, there is a tendency for the *T. inter-*

TABLE I

Mortality of host and parasites exposed in the laboratory to various temperature sand periods of time

Treatment		Control		−21°C. for 72 hrs.		−21°C. fro 168 hrs.		−23°C. for 12 hrs.		−28°C. for 12 hrs.	
Species		living	dead	living	dead	living	dead	living	dead	living	dead
R. buoliana		336	18	80	9	44	50	77	39	16	445
O. obscurator	living	129	—	37	—	19	—	32	—	3	—
	dead	—	3	—	2	—	21	—	11	—	154
T. interruptor	living	13	—	9	—	3	—	4	—	—	—
	dead	—	—	1	1	—	3	2	10	—	48
% parasitism		42	17	59	33	50	42	49	54	20	45

TABLE II

Field mortality of host and parasites above snow level during the winter of 1958-1959

Date of collection		Oct. 31		Dec. 6		Jan. 7		Feb. 17	
Minimum temperature		−3°C.		−18°C.		−25°C.		−26°C.	
Species		living	dead	living	dead	living	dead	living	dead
R. buoliana		205	14	117	9	50	150	9	174
O. obscurator	living	85	—	45	—	19	—	1	—
	dead	—	2	—	1	—	62	—	50
T. interruptor	living	9	—	7	—	1	—	—	—
	dead	—	—	—	—	1	7	—	17
% parasitism		46	14	44	11	42	46	11	39

TABLE III

Field mortality of host and parasites at three crown levels in the spring of 1959

Crown levels (ft.)		0−2		2−4		4−6		Total	
Species		living	dead	living	dead	living	dead	living	dead
R. buoliana		74	26	34	66	6	94	114	186
O. obscurator	living	29	—	10	—	4	—	43	—
	dead	—	7	—	23	—	33	—	63
T. interruptor	living	5	—	3	—	1	—	9	—
	dead	—	—	—	9	—	12	—	21
% parasitism		46	27	38	48	83	48	46	45

ruptor population to be reduced in relation to the surviving host population because of its preference for the upper crown levels of the infested trees, where host mortality is high in severe winters, and also because of its lesser resistance to low temperatures.

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Notes on Life-History and Taxonomy of *Ceruraphis eriophori* (Wlk.) and *Neoceruraphis viburnicola* (Gill.), and a Description of the Apterous Viviparous Female of *Neoceruraphis viburnicola* (Gill.) (Homoptera: Aphididae)[1]

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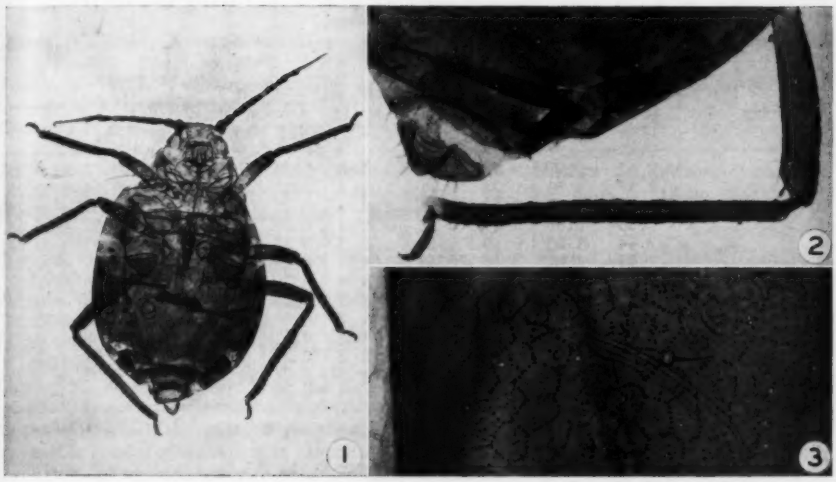
In New Brunswick, *Ceruraphis eriophori* (Wlk., 1848) and *Neoceruraphis viburnicola* (Gill., 1909) are readily found in spring and autumn on their *Viburnum* hosts. I have collected both species from the curled leaves of these primary hosts (*C. eriophori* from *Viburnum lantana* L. and *V. opulus* L. and *N. viburnicola* from *V. opulus* var. *roseum* L. and *V. trilobum* Marsh.) In Colorado, Palmer (1952) recorded both species from *V. opulus* var. *sterile* (= *V. opulus* var. *roseum*).

The known secondary host plants of *C. eriophori* in Europe are species of *Carex*, *Eriophorum*, *Luzula*, and *Typha* (Börner, 1952); in North America, *Cyperus virens* Michx. is the only one reported (Palmer, 1952). The secondary hosts of *N. viburnicola* have not been recorded (Palmer, 1952; Shaposhinkov, 1956), nor has the apterous viviparous female been described.

In June 1957 and 1959, I transferred both species from their *Viburnum* hosts to *Carex pallescens* var. *neogaea* Fern. and to *Scirpus rubrotinctus* Fern. Colonies of apterae developed in the greenhouse on these plants just above the soil level between the leaf blades. Summer apterae of *N. viburnicola* were readily distinguished from *C. eriophori* by their colour and by the absence of the white tuft of wool before the cauda. During the summer of 1959, I examined hundreds of sedges growing in and around Fredericton. *C. eriophori* was collected four times and only from *S. rubrotinctus* but *N. viburnicola* was not found.

The nomenclature of these two species has been confused by some authors. Gillette (1909) described as new *Aphis viburnicola* from Colorado. Börner (1916), apparently unaware of Gillette's publication, described as new *Aphis viburnicola* from Germany. Later, in 1926, Börner mistakenly considered that these were one species and placed it in his new genus *Ceruraphis*. But Franssen (1927) showed that *viburnicola* Gill., 1909, and *viburnicola* Börner, 1916, are

[1]Contribution No. 5, Research Station, Canada Department of Agriculture, Fredericton, New Brunswick.



Figs. 1-3, *Neoceruraphis viburnicola* (Gill.), apterous viviparous female from *Scirpus rubrotinctus* Fern. 1, Apterous viviparous female. 2, Hind tibia bearing sensoria. 3, Cell-like reticulation on integumentum showing spinules and a seta.

distinct species; he proposed the name *viburniana* Franssen for *viburnicola* Börner should the two species fall in the same genus. In spite of this Börner (1930) continued to refer to both species as one and wrote "*C.* (*Aphis*) *viburnicola* Gill., Börn. = *eriophori* Wlk." Later Börner and Schilder (1932), although they referred to Franssen (1927), still listed both *viburnicola* Gill. and *viburnicola* Börner as synonyms of *eriophori* Wlk. Gillette and Palmer (1932) stated that *viburnicola* Gill. could not be considered a synonym of *eriophori* Wlk. Finally, in 1952, Börner agreed that *eriophori* Wlk. and *viburnicola* Gill. are distinct and placed them both in the genus *Ceruraphis* Börner, 1926. Shaposhnikov (1956) erected the genus *Neoceruraphis* for *viburnicola* Gill. Although the two species, when all morphs are considered, are similar in life history, habits, and morphology, a generic division seems to be justified on the basis of the spinulose siphunculi of *N. viburnicola* (Gill.) and the imbricated siphunculi of *C. eriophori* (Wlk.).

In his description of the various morphs of *N. viburnicola*, Shaposhnikov (1956) stated that the migrants have prominet abdominal tubercles. Although these tubercles are present in the spring migrants, none of the autumn migrants that I examined had marginal or spinal tubercles. It seems that Shaposhnikov based his description only on the spring migrants. He also stated that the migrants and males have pseudosensoria on the hind tibiae. In my specimens, I found pseudosensoria on the hind tibiae of the spring migrants but not always on the hind tibiae of the autumn migrants or of the males.

Gillette (1906) described all morphs of *N. viburnicola* except the apterous viviparous female. The following description of that form is based on specimens that I reared on *Scirpus rubrotinctus* Fern., in 1957 and 1959.

Apterous Viviparous Female (Fig. 1).—Body in life slightly powdery; newborn nymph pale pink to purplish; newly developed adult with deep-pink head and cream-coloured abdomen; older adult with pink head, brownish dorsally and pink ventrally on abdomen. Body oval-ellipsoid. Integumentum with dis-

Measurements in mm.

No.	Length body	Ant.	Siph.	Cau.	Rhin. on III	Ant. segments			
						III	IV	V	VI
1	2.42	0.99	0.22	0.09	3 & 4	0.25	0.13	0.13	0.08 + 0.25
2	2.37	1.01	0.22	0.11	2 & 4	0.27	0.14	0.13	0.08 + 0.25
3	2.28	0.96	0.19	0.12	3 & 4	0.25	0.12	0.12	0.07 + 0.24
4	2.25	0.99	0.17	0.11	0 & 1	0.27	0.13	0.13	0.07 + 0.25
5	2.44	1.05	0.19	0.11	1 & 1	0.27	0.14	0.15	0.09 + 0.24
6	1.95	1.02	0.16	0.10	2 & ?	0.28	0.12	0.13	0.07 + 0.25
7	2.11	1.10	0.19	0.13	3 & 4	0.30	0.14	0.14	0.08 + 0.27
8	1.89	0.90	0.14	0.11	1 & 1	0.25	0.09	0.15	0.08 + 0.23
9	2.13	1.03	0.19	0.13	0 & 3	0.30	0.11	0.12	0.08 + 0.25
10	2.29	1.04	0.17	0.11	1 & 2	0.27	0.14	0.13	0.08 + 0.25
11	2.06	1.02	0.18	0.08	1 & 3	0.25	0.14	0.12	0.09 + 0.25
12	2.24	1.08	0.18	0.13	2 & 3	0.27	0.14	0.13	0.08 + 0.29

(1-12, from *Scirpus rubrotinctus* Fern., Fredericton, N.B., M. E. MacGillivray; 1-4, 9-VII-1957; 5-12, 2-VII-1959).

Morphotypes, apterous viviparous female, No. 6971, in the Canadian National Collection of Insects, Ottawa, Canada.

tinct cell-like reticulation; each cell bordered by minute spinules, with several nodules or spinules of the same type inside each cell (Fig. 3). Tergum sclerotic, with abdominal tergites I-VII coalesced; tergum pigmented, light brown. Dorsal hairs numerous; those on anterior abdominal segments one-half to three-fifths of basal diameter of third antennal segment, those on eighth segment 2 to 3 7/11 times that diameter; marginal hairs also numerous. Small spinal tubercles sometimes on abdominal segment VII; rather large, flattish marginal tubercles on prothorax and abdominal segments I-V. Head with scattered spinules, which do not have a cell-like arrangement; front flat with about the normal number of hairs which are 1 1/4 to 2 3/11 times basal diameter of third antennal segment. Antenna of 6 segments; nearly half as long as body; black except the processus terminalis, which is pale; third segment with 0-4 irregularly placed rhinaria; hairs stiff and conspicuous, those on inner side longer than those on outer side; longest hairs on third segment 1 1/4 to 2 3/11 times basal diameter of that segment. Rostrum short, just reaching middle coxae; last segment 0.17 to 0.18 mm: long, with two to five hairs besides the three apical pairs. Siphunculus similar to that of the alatae, covered with rows of minute spinules; black, tapering, with a distinct wide flange; basal diameter 1.7 to 2.5 times smallest diameter just before the flange; flange 1.4 to 1.7 times as wide as that smallest diameter. Cauda dark, rounded, slightly tapering at distal end but not tapering as much as in the alatae; hardly longer than wide; with 10 to 12 long, curved hairs. Legs dark throughout except basal half of fore femur which is pale; femora with numerous stiff hairs; hind tibia slightly wider than other tibiae, with 35 to 70 pseudosensoria on distal three-quarters (Fig. 2); first tarsal joints with four hairs; second joint of hind tarsus 0.11 to 0.12 mm. long.

Acknowledgments

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Life History and Behaviour of the Leafhopper *Macropsis fuscula* (Zett.) (Homoptera: Cicadellidae) in British Columbia[1]

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Macropsis fuscula (Zett.), which is a species common in Europe, was first reported in North America in 1952 when specimens were collected from loganberry on Lulu Island, British Columbia. High infestations persisted on Lulu Island until the destruction of most of the loganberry canes there during a severe freeze in November, 1955. New cane growth was normal in 1956, but no leafhoppers could be found. Only a few nymphs were found in 1957, but there was an average of 14 nymphs per 100 fruit buds in 1958, and 48 nymphs in 1959, compared to 32 nymphs during the last season of high infestations in 1955. Reinfestation from hardy wild hosts common in the area probably largely accounts for the rapid re-establishment of this pest on cultivated loganberry.

De Fluiter and van der Meer (1956) summarized the life history of *M. fuscula* in the Netherlands. The seasonal development of this leafhopper in British Columbia is similar to that in the Netherlands. In both areas there is one generation each season, and overwintering occurs in the egg stage. The present paper is based on work conducted on Lulu Island, British Columbia, from 1952 to 1959.

Economic Importance

De Fluiter and van der Meer (1953, 1956) demonstrated that *M. fuscula* is a vector of rubus stunt virus of raspberry in the Netherlands. This disease, which causes dwarfed, weak, non-fruiting canes, is common in England and the Netherlands on loganberry, raspberry, blackberry, and other species and hybrids of *Rubus,* but has not been reported in North America.

[1]In part from a thesis presented in partial fulfilment of the requirements for the M.S. degree at Oregon State College, June, 1959.

In British Columbia leafhopper nymphs were present on or near the fruit throughout the harvesting period of loganberry. When infestations were high, quantities of honeydew were excreted. The sooty fungus that grew in this spoiled the appearance of the berries. Moreover, nymphs that remained on the fruit after picking became a contamination problem in processing.

Infections of leaf spot disease, *Mycosphaerella rubi* Roark (*Septoria rubi* West.), masked any direct injury from leafhopper feeding. However, there was some indication that scarring occurred when nymphs fed directly on the berries. Adults, which fed mainly on the new growth, did not cause any significant injury to the canes.

Distribution in British Columbia

Since its appearance in 1952, *M. fuscula* has spread from Lulu Island eastward into the lower Fraser Valley, and by 1959 was present on cultivated and wild hosts in the Abbotsford and Yarrow districts 50 miles from the original site of infestation. Specimens were collected in 1955 from loganberry at Saanich on southern Vancouver Island.

Hosts

Collections of *M. fuscula* were made from cultivated loganberry, *Rubus loganobaccus* Bailey; boysenberry, *Rubus* spp.; red raspberry, *R. idaeus* L. varieties Washington, Willamette, and Newburgh; thimbleberry, *R. parviflorus* Nutt.; wild cutleaf blackberry, *R. lacineatus* Willd.; and Himalaya blackberry, *R. procerus* Muell.

Large numbers of leafhoppers occurred on loganberry and boysenberry. Small numbers were observed on raspberry next heavily-infested loganberry, and on raspberry isolated from heavy infestations. Only light infestations were found on thimbleberry. Wild blackberries generally supported moderate to heavy infestations.

Methods

Nymphs of *M. fuscula* were collected from a loganberry planting at three- to four-day intervals during June, July, and August, 1955. At least 100 specimens were taken on each date. The nymphs in each collection were separated according to instars, and records kept of the date when the first individuals of each instar appeared, the peak abundance period, and the date when the last individuals of each instar were collected. Nymphs of the third, fourth, and fifth instar were also separated according to sex by examining the genitalia.

Observations on the rate of development of nymphs under field conditions were made during 1956 and 1957 using newly emerged individuals caged on the bud clusters of loganberry, raspberry, thimbleberry, and wild blackberry. Screened, bivalve cages, of plastic (Fig. 1) about 1½ inches in diameter were used. Nymphal growth was determined by examining the cages for cast skins at two-day intervals.

Egg

The egg (Fig. 2) averages 1.2 mm. in length and .4 mm. in diameter, and is translucent white, subcylindrical, elongate, slightly curved, with a broadly-rounded base and tapered to the apical end.

The eggs are laid in the bark of the young canes, usually in the fleshy region of a leaf node or at the base of a thorn. There is no particular orientation with the grain of the wood, there is frequently no external indication of the presence of eggs within the canes, but sometimes there are raised, blister-like areas over the eggs, or the tips are exposed, particularly when the eggs are laid in crevices or folds.

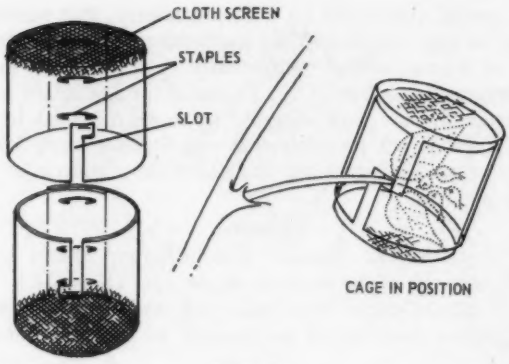


Fig. 1.

Hatching usually began during the last half of May, but started in early May in the exceptionally warm seasons of 1957 and 1958. Nymphs continued to emerge for five to six weeks, with a peak during the second or third week.

Kunkel (1933) stated that eggs of *M. trimaculata* are dormant when deposited and apparently require exposure to low temperatures for development to start. Experiments on the eggs of *M. fuscula* indicated that the incubation period was shortened by exposure to low temperatures but that the duration and intensity of cold required were relatively moderate.

Eggs in blackberry canes collected in mid-December, 1957, and exposed in the laboratory to 37° F. for 7, 14, and 21 days started to hatch within 27, 24, and 16 days respectively when removed to fluctuating room temperatures of 51° to 86° F., compared to an incubation period of 30 days for eggs in canes kept throughout at the higher temperatures. Eggs in canes exposed for one day to 28° F. started to hatch in 20 days at a constant temperature of 68° F. compared to 25 days for eggs in canes kept throughout at constant temperature.

Eggs in canes collected in early February, 1958, and exposed to 20°, 24°, or 28° F. for intervals of 1, 3, 6, and 10 days showed no differences in incubation periods at a constant temperature of 68° F. for any of the temperature ranges or exposure intervals, nor was there any difference in the incubation periods of eggs between those receiving an interval of cold exposure in the laboratory and those held throughout at a constant temperature. Egg hatching started in all these canes within 15 to 17 days.

Canes collected in mid-December and early February during the winter of 1957-58 had been subjected to low temperatures in the field, but the season was exceptionally mild, with little freezing weather. However, by the beginning of February the eggs had received sufficient exposure to low temperatures to enable development to begin. Presumably in a more normal winter, with colder temperatures, the necessary exposure interval would be completed even earlier. Apparently winter temperatures do not exert any marked effect in determining the date of hatching, but this date is influenced mainly by the temperature ranges that occur during the early spring before hatching.

The destruction of most of the loganberry canes on Lulu Island during a severe freeze in early November, 1955, has been mentioned previously. Egg mortality from the direct effect of low temperatures was not responsible for the lack of infestations on this host during the following season, as leafhoppers

were present in normal abundance on wild blackberry, that survived the freeze. In the laboratory no eggs hatched from cane sections that were dried to simulate the after-effects of winter killing. Apparently eggs protected in the canes can withstand air temperatures as low as 10° F., but if the host plant is killed the eggs are destroyed, probably by desiccation or by being crushed by the shrinking plant tissues. Thus it is not probable that egg-bearing canes killed during the dormant season but remaining in the field provide a source of infestation for adjacent healthy plants.

Nymph

There are five nymphal instars. The different instars are readily distinguished by the diameter of the head across the eyes (Figs. 3-7).

Colour in all instars varies from pale yellowish to greenish or tan; some individuals are stippled dark brown or blackish to give a general dark fuscous appearance.

Nymphs feed mainly on the stems and on the bases of the calyces of flower buds and fruit. Nymphs have also been observed feeding on the fruit drupelets and on the midribs on the undersides of the leaves.

In 1955 individual nymphs required an average interval of 10 days to complete each of the first to the fourth instars, and 15 days for the fifth instar. There was much overlapping of instar groups in the field as the season progressed (Fig. 10); first-instar nymphs were still emerging when some of the earliest nymphs had reached the fourth instar. All nymphs had completed development by the end of August.

The average time from the first appearance of nymphs to the first adults varied considerably in different seasons, depending on temperatures during development. The dates of appearance of first nymphs and adults during the seasons of 1954 to 1958 were as follows:

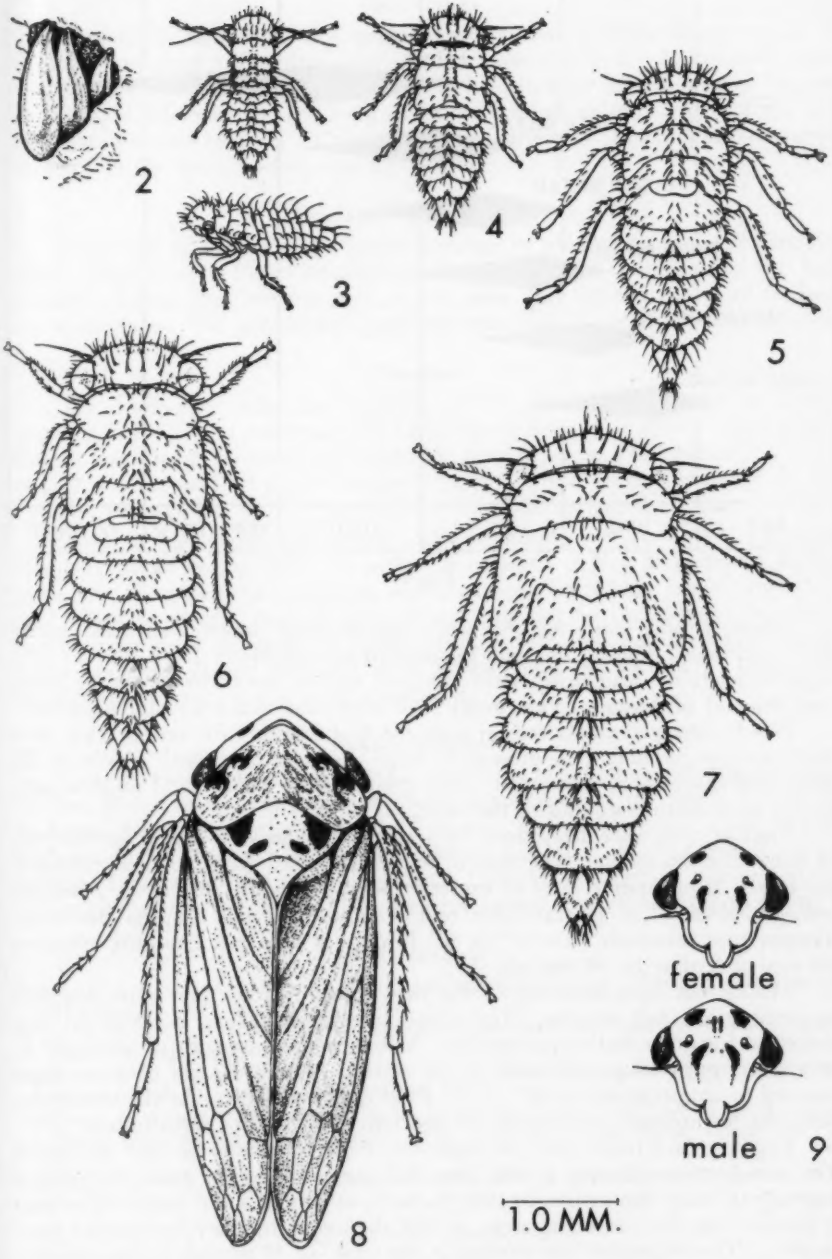
	1954	1955	1957	1958
Average temperature for May, June, and July (18-year average 58.7° F.)	57.3° F.	56.0° F.	60.3° F.	64.0° F.
First nymph	May 28	May 28	May 15	May 10
First adult	July 20	July 21	June 24	June 16
Total duration of instars	53 days	54 days	40 days	37 days

The effects of temperature on the rate of development were observed on laboratory-reared nymphs. Those reared at a constant temperature of 68° F. became adults in an average period of 29 days; those reared at fluctuating room temperatures with a mean of 71.7° F. became adults in 27.5 days. Nymphs placed in an insectary at a mean temperature of 47.7° F. failed to develop beyond the first instar: one first-instar nymph moulted after 20 days but died later, whereas others had not moulted after 35 to 44 days when observations were discontinued.

Adult

The body length is 4.0-5.0 mm. (Fig. 8). General colour greyish-yellow, the male darker than the female. The black spot at the base of each hind tibia and the characteristic facial markings (Fig. 9) are distinctive features of *M. fuscula*. Beirne (1954, 1956) described the adult.

Adults appeared during late June and in July, and continued to emerge until the end of August or early September. They were most abundant during mid-August, but decreased rapidly towards the end of September. Very few were present by mid-October, and none was found after the end of October.



Figs. 2-9.

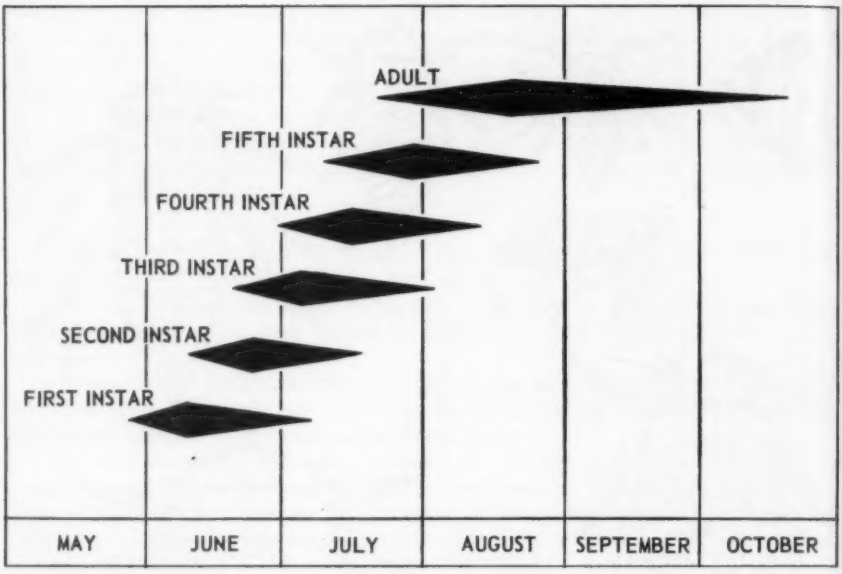


Fig. 10

There is some indication that adult females lived longer than males under field conditions. During the high infestations on loganberry from 1952 to 1955 large numbers of dead males were common on the lower leaves of the canes near the end of August. Few males have been observed after mid-September.

Newly emerged adults remain near the fruit clusters for one or two days then move to the new cane growth to feed. Females frequently remain at the same feeding site for several hours. The preferred site was at a leaf node, usually on the more mature sections of the canes.

Feeding rates were determined for several individuals by timing the intervals of honeydew excretion. The rate of excretion varied from 10 to 60 droplets per hour. Comparative rates of excretion of the meadow spittlebug, *Philaenus leucophthalmus* (L.), on the same host were 420 to 480 droplets per hour. Temperature variations from 60° to 80° F. did not appear to have any effect on the rate of feeding by *M. fuscula.*

Mating has been observed in the field three or four days after the first appearance of adult females. The actual mating procedure is similar to that described for other leafhopper species. Mating couples remain paired for 40 to 80 minutes at air temperatures of 70° to 74° F. Mating did not occur in cages exposed to temperatures of 85° to 95° F. in direct sunlight. At these temperatures the leafhoppers are very active and sensitive to slight disturbances.

Eggs are laid from noon to dusk, but most frequently in late afternoon. The female ceases feeding at this time and moves along the cane, stopping at intervals to insert the ovipositor into the bark, usually at a leaf node. This part is fleshier than the internodal areas, so that the ovipositor may be inserted more readily. The ovipositor was inserted in the cane for 45 seconds to five minutes. The longer intervals may indicate deposition of several eggs in the same site; in several instances the ovipositor was partially withdrawn and then reinserted. Four or five eggs were found side by side in the cane tissue.

Sex Ratios

Most of the first adults that appeared were males; females did not appear in numbers until four or five days after the first males emerged. An equal sex ratio was present when the population reached a peak, after which females became increasingly predominant, and most of the individuals collected toward the end of the season were females. The same general pattern of sex ratios also occurred throughout the third, fourth, and fifth instars.

Predators and Parasites

There was no evidence of effective predator or parasite action on *M. fuscula*. Dead nymphs were found occasionally in the webs of spiders near the bud clusters. Nabid bugs were present on the canes, but did not appear to feed on the leafhoppers. No parasitized specimens were found in rearings or collections.

Summary

The leafhopper *Macropsis fuscula* (Zett.) was first reported in North America in 1952 from loganberry on Lulu Island, British Columbia. Host plants include loganberry, boysenberry, raspberry, blackberry, and thimbleberry. Fruit quality was reduced by a sooty fungus that grew in honeydew excreted by the nymphs, and nymphs were present as a contaminant on harvested fruit.

There is one generation a year. Overwintering occurs in the egg stage. Hatching began during May. A period of exposure to low temperature during the winter shortened the incubation period of eggs, but winter temperatures had little effect in determining the date of egg hatching in the spring. Nymphal development rates increased at higher temperatures, but ceased below 50° F. Adults appeared during July and were present until late October. There was no effective control by predators or parasites.

Acknowledgments

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Control of Adult Black Flies (Diptera: Simuliidae) in the Forests of Eastern Canada by Aircraft Spraying[1]

By D. G. PETERSON[2] AND A. S. WEST[3]

Introduction

A study of the biology and control of black flies in the forests of Eastern Canada was conducted on the north shore of the St. Lawrence River, near Baie Comeau, Quebec, from 1954 to 1956. Reference was made to this study by Peterson and Wolfe (1958). Details on the identity of species, and studies on their life histories and habits were reported by Wolfe and Peterson (1959), while the control of black-fly larvae by aircraft spraying was described by West, Brown, and Peterson (in press). Experiments on the control of adult black flies by aircraft spraying are reported in this paper.

The terrain in the Baie Comeau region is rugged, with narrow, deep valleys separated by smooth, round ridges with steep, rocky slopes. Lakes, streams, and rivers are numerous. It is typical of the Canadian shield. The vegetation is mixed coniferous and deciduous with spruce, balsam fir, jack pine, alder, poplar, and large stands of birch that have been ravaged by die-back. It is often impractical in heavily forested or otherwise difficult terrain, such as this, to apply control measures on the ground against adult biting flies, including black flies. In similar circumstances in northern Canada, aircraft spraying provided a practical and effective method of control (Twinn, 1950). Area control of adult mosquitoes in northern Canada by spraying with a Douglas Dakota (C-47 or DC-3), fitted with a vertical emission pipe, was reported by Twinn, Brown, and Hurtig (1950). Brown *et al.* (1951) conducted a large-scale experiment with similar equipment at Goose Bay, Labrador, for the control of adult mosquitoes and black flies. It was reported that adult black flies were killed by a spray of 4.2 per cent DDT in oil applied at an average rate of 0.165 lb. of DDT per acre. In 1952, Brown reported the results of further experiments in Labrador with a similar aircraft but fitted with a rotary brush rather than the vertical emission pipe. An average reduction of not less than 80 per cent of the adult black-fly population was reported when 10 sq. mi. of spruce forest were treated with a 10 per cent solution of DDT in oil at 0.22 lb. of DDT per acre, while a 20 per cent solution applied at 0.27 lb. per acre reduced the population by 87 per cent. The effect of the control of adult mosquitoes and black flies by aircraft spraying was transitory, since the treated areas were re-infested by adult flies flying in from beyond the perimeter of the sprayed area. In spite of this limitation, several weeks' protection from the attack of the biting flies was obtained.

A further study of the efficacy of aircraft spraying in the control of adult black flies, as well as an assessment of a light aircraft as compared to the larger DC-3, was made possible by an offer of the Quebec North Shore Paper Company, Baie Comeau, Quebec, to make available a DHC-2, Beaver, aircraft fitted for spraying. The locale of the study was the village of Franquelin, situated on a raised beach at the mouth of the Franquelin River, approximately 12 miles east of Baie Comeau. Paralleling the shore in this region is a rocky cliff that, from the mouth of the Franquelin river, runs behind the village at a height of several

[1]The results herein reported were obtained by the former Veterinary and Medical Entomology Unit, Entomology Division, Department of Agriculture, Ottawa, Canada, in a program of studies carried out on behalf of the Pulp and Paper Association of Canada, and in co-operation with the Pulp and Paper Research Institute of Canada, Montreal, Quebec.

[2]Entomology Laboratory, Research Branch, Canada Department of Agriculture, P.O. Box 248, Guelph, Ontario.

[3]Department of Biology, Queen's University, Kingston, Ontario; in the seasonal employ of the Canada Department of Agriculture, as Entomologist, when part of this work was performed.

hundred feet. The interior is heavily forested and is characterized by the deep, narrow, valleys of the Franquelin, Mistassini, and lesser rivers and streams.

Simulium venustum Say was the principal pest species. Limited numbers of the *Prosimulium hirtipes* Fries complex were present.

Materials and Methods

In 1954, a DHC-2, Beaver aircraft, equipped with floats, was used for the application of the spray. It was fitted with a tank, 20 in. long, 46 in. wide, and 36 in. high, and with a capacity of 110 gal. A rotary brush unit (I-C-D Series 800) was mounted at each end of a 13-ft. steel boom, 2 in. in diameter, that crossed underneath the fuselage at a level 64 in. below the wing. Each rotary unit carried two 10-in. circular brushes alternating with two 8-in. brushes, and was turned at an estimated 2,500 r.p.m. by a wooden propeller, 22 in. in diameter and with a 30-degree pitch. The supply of spray was controlled by one-inch Whittaker valves at the junction of each rotary unit with the boom, and cables carried forward to a shut-off lever and a quadrant controlling orifice size, both located in the cockpit. The emission rates of the rotary brush assembly were determined on the ground and in the air. A rate of 0.37 g.p.s. was selected to give an intended dosage of 0.21 lb. of DDT per acre on the basis of a flying speed of 95 m.p.h., a 200 yd. interval between flight lines, and an 11 per cent (wt./vol.) solution of technical DDT in oil. The solution was prepared by diluting one part of Jp-30 concentrate with 2 parts of furnace oil.

The area sprayed in 1954 is shown in Fig. 1. A similar map was prepared for the aircrew, showing the magnetic bearing, location, and length of the flight lines on which the DDT solution was to be dispersed to completely cover the area. The shore line was used as the base line for the majority of runs. The high cliff behind the village necessitated four short runs at right angles to the remainder. Spraying commenced at 1155 hrs. on July 8, a heavily overcast day, and was completed by 1815 hrs. A total of 742 gal. of the 11 per cent solution were dispersed over an area of 6.7 sq. mi. to give an actual dosage of 0.19 lb. of DDT per acre, 0.02 lb. per acre less than intended.

In 1956, two Stearman biplanes, each fitted with a 125-gal. tank and a boom spray assembly with 22 spray-cone nozzles under positive pressure, were made available under contract[4]. The spray plan used in 1954 was altered slightly in 1956 to avoid the application of any DDT on the drainage of the Mistassini River, at the lower end of which there is a fishing camp. As a result, a 10 sq. mi. plot of irregular shape, was treated. The approximate distances from Franquelin village to the boundaries of the spray lot were 1¼ miles to the west and north, two miles to the east, and three miles to the northeast. Parallel flight lines at 200 yd. intervals were flown as before. The spraying was completed in two hours on the evening of July 6, under nearly ideal weather conditions. An 11 per cent solution of DDT was prepared in the same manner as in 1954. The dosage was 0.22 lb. of DDT per acre.

Thirty check points were established in 1954 (see Fig. 1) for the assessment of the level of black-fly activity prior to, and following the spraying. The number of points was limited by the inaccessibility of the area. Ten check points were inside the sprayed area. The remainder were beyond the perimeter, twelve to the northeast and eight to the northwest. The latter were so close to the perimeter that, under the weather conditions prevailing at the time of the experiment, it was considered possible that some of the spray reached these points. The data collected there was not used in the analysis of the results.

[4]Wheeler Airlines, Ste. Jovite, Quebec.

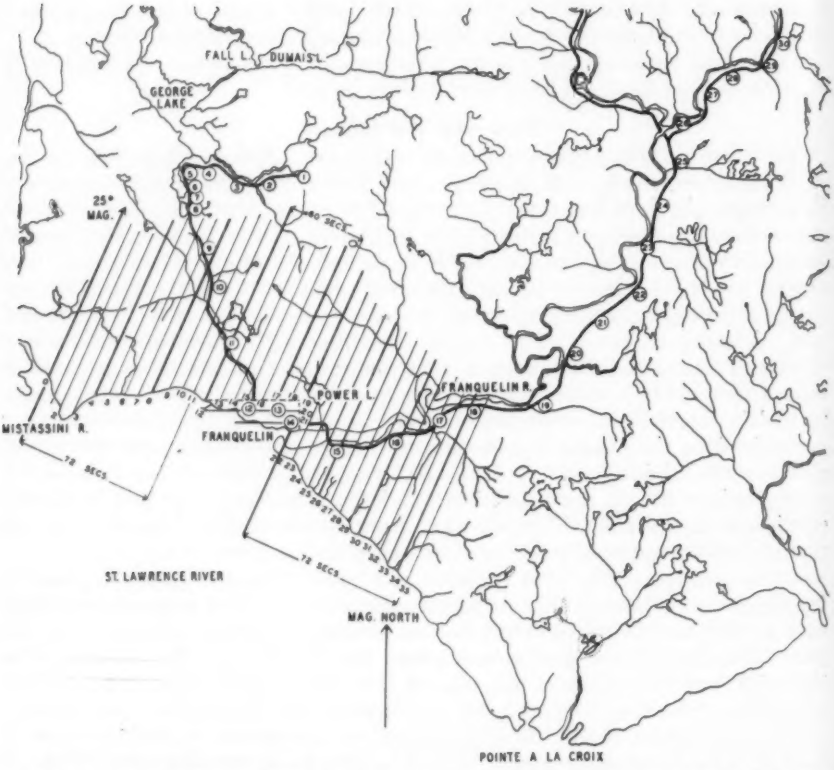

Fig. 1. Map of Franquelin, Quebec, showing spray plot layout used in 1954, including lines of flight of aircraft, the direction of flight, and check points inside and outside the sprayed area.

Paired counts were made daily from July 2 to 21 by two observers at each of the check points, commencing at No. 1 and progressing to No. 30. At a check point, the observers sat, spread an 18-in. square of dark blue flannel, and, after a two-minute wait, made a one-minute count of the number of black flies contacting the surface of the cloth.

Essentially the same pattern of check points was used in 1956. Eighteen stations were selected within the sprayed area and 16 beyond the perimeter, to the west, north, and northeast. None of the check points beyond the perimeter were closer than one-half mile to it. The check points were visited daily in a consistent order. Pre-spray counts were made for a 10-day period, and post-spray counts were continued for 21 days.

Results

The pre- and post-spray levels of black-fly activity in 1954 and 1956 are shown graphically in Fig. 2. The levels of activity within and beyond the perimeter of the sprayed area are represented, respectively, by the arithmetic means of the averages of the two simultaneous counts at the check points within, and those beyond the perimeter.

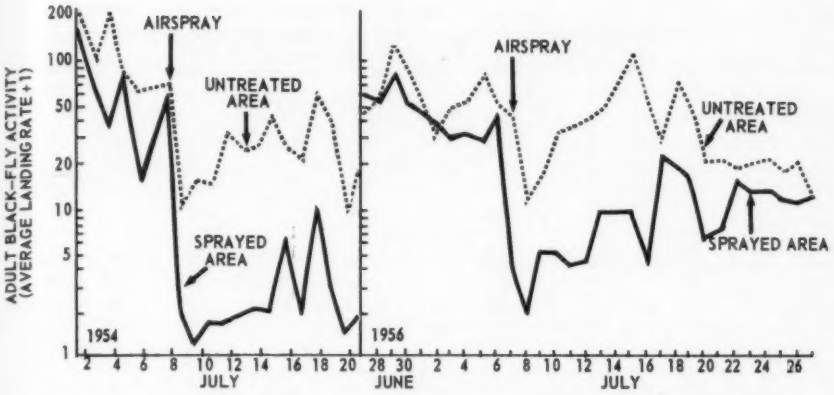

Fig. 2. The effect of aerial applications of DDT on infestations of adult black flies at Franquelin, Quebec, in 1954 and 1956

Many variable factors were introduced by the limitation imposed by visiting a series of stations at different times of the day; by the effect of the wet season on the validity of the sampling; and, by the fact that all stations were not visited on a number of days. However, a simple comparison is given in Table I. Although the maxima tended to occur more frequently in certain areas, this trend was not consistent, an observation that would be expected in view of the variables imposed by meteorological conditions.

Discussion

The conditions under which the experiments were conducted were not ideal. In 1954, the aircraft spraying was conducted during a general decline in black-fly activity associated with the onset of a six-week period of comparatively heavy rainfall. In 1956, black-fly activity was at a low level throughout the summer, again associated with inclement weather. Activity declined generally at about the time the spray was applied.

Seasonal changes in black-fly activity, and those associated with meteorological conditions, prohibit the expression of the efficacy of the sprays in quantitative terms, e.g., as a per cent control based on levels of activity within the sprayed area. It was evident in 1954, however, that the aerial application of DDT was effective in the control of adult black flies. The black-fly population in the sprayed area fell well below the level at which it is considered to be a problem. Within the village, the centre that was to be protected, black flies were almost entirely eliminated. They were not observed in this area until the tenth day following the application. All evidence suggests that a reduction in black-fly activity also occurred as a result of the spray application in 1956. No complaints of black-fly activity within the village of Franquelin itself were received during the first 10 days following the spray application. Thereafter, flies were a nuisance at times.

The duration of the period of protection afforded to the village is difficult to assess. It is conditioned by the actual control achieved by the spray, the extent of the sprayed area, the rate of movement of flies into the sprayed area, i.e., rate of reinfestation, as well as the meteorological conditions obtaining during the post-spray period. In 1954, black flies never became a problem after the spraying.

TABLE I
Adult black-fly activity before and after an aerial application of DDT at 0.22 lb. per acre at Franquelin, Quebec, July 6, 1956.

Date	Landing rates*	
	Sprayed area	Check area
June 27	423	178
28	270	167
29	324	382
30	152	191
July 1	106	155
2	109	109
3	185	221
4	129	188
5	134	166
6	173 Av. = *200.5*	158 Av. = *191.5*
7	30	242
8	12	51
9	19	65
10	55	61
11	14	179
12	10	216
13	58	194
14	–	–
15	52	1,008
16	12 Av. = *29.1*	352 Av. = *263.1*
17	107	80
18	113	350
19	63	106
20	25	43
21	28	84
22	53	70
23	45	67
24	51	57
25	63	65
26	40	55
27	36 Av. = *56.7*	38 Av. = *92.3*

*Each figure is the highest of the mean landing rates obtained during the daily observations at 18 assessment stations in the area sprayed and at 16 stations in a check area.

The unfavourable weather appeared to prolong the protection achieved by the spraying. The flies became a nuisance more than 10 days after the spraying in 1956, in spite of continuing inclement weather.

Summary

In 1954, an 11 per cent solution of DDT in furnace oil was applied from a DHC-2, Beaver aircraft fitted with a rotary-brush assembly, to an area of 6.7 sq. mi. at the village of Franquelin, Quebec, for the control of adult black flies. A dosage of 0.19 lb. of DDT per acre significantly reduced the adult black-fly population. An application of the same material at 0.22 lb. of DDT per acre to an area of 10 sq. mi. in 1956, by two Stearman biplanes fitted with boom-spray assemblies, reduced the number of black flies for a period of more than 10 days.

Acknowledgments

Grateful acknowledgment is made of the assistance of A. W. A. Brown, Department of Zoology, University of Western Ontario, London, Ontario, in preparing for the experiment in 1954; the assistance of H. S. D. Swan, Woodlands Department, Pulp and Paper Research Institute of Canada in securing the

co-operation of member companies of the Association, and, together with J. F. Sharp, Veterinary and Medical Entomology Unit, Department of Agriculture, Ottawa, in arranging many details of supply and administration; the valuable co-operation received from H. A. Sewell, Vice-President, Ontario Paper Company, and T. B. Fraser, Manager, and other officers of Woods Department, Quebec North Shore Company; and, the assistance in the spray operations and assessments by J. A. Armstrong, B. E. Lanning, J. A. Roe, M. W. Newediuk, and J. E. P. Trudel, student assistants.

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Book Reviews

Obligatory and Facultative Insects in Rose Hips. Their Recognition and Bionomics. By W. V. Balduf. Illinois Biol. Monographs No. 26, 194 pp., 12 plates. 1959. University of Illinois Press, Urbana, Ill. Price $3.50.

In these days when most entomological research aims at the control of insects, or at the elucidation of general biological principles using insects merely as tools, an extensive study of a group of insects simply for their intrinsic interest is uncommon. The author's leisurely style is also uncommon in scientific works.

For ten years Dr. Balduf collected rose hips in Illinois and other central states, and correspondents sent him collections from Maine to California and Alaska in the United States and from three Canadian provinces. He reared their insect inhabitants and studied the habits and life-histories of the commoner species in considerable detail. Five primary species, *Rhagoletis basiola* (Osten Sacken), *Cydia* (*Grapholitha*) *packardi* (Zell.), *Rhynchites bicolor* (Fabr.), *Megastigmus aculeatus* (Swederus), and *M. nigrovariegatus* Ashm., feed within the hips. These are hosts of a total of ten hymenopterous parasites, and about ten other parasites emerged from hips but their particular hosts are unknown. Two predators also occurred, and a dipteron and a mite were scavengers in hips infested with other species. The various stages of the principal species are described in enough detail to allow their recognition.

Dr. Balduf has supplemented his own studies on the American species by a thorough coverage of the literature, and also has included summaries of published work on several European insects of similar habits, to give an up-to-date account of all insects known to normally inhabit rose hips. It is illustrated by excellent drawings.

WM. L. PUTMAN

Production of the Agamic Form of the Spotted Alfalfa Aphid, *Therioaphis maculata* (Buchton). By J. P. Paschke, 50 pp., 14 figs. University of California Publications in Entomology 16. 1959. Price $1.00.

The factors influencing the production of alate viviparous forms in aphid populations have been the subject of considerable experimentation. This publication deals with a series of field and laboratory experiments designed to investigate more thoroughly most of the factors considered to have some degree of influence on the production of alate viviparous forms. The factors investigated include the effects of: photoperiod, starvation, age of leaf, nutrient deficiencies of host plant and high population density. The conclusions, largely based on statistical analyses, are generally negative for all but the last two factors. A percentage increase in the number of alatae was demonstrated in populations fed on plants known to be deficient in potassium and phosphorus, and also in experiments designed to test only the effects of crowding. Experiments were also designed to detect the developmental stage at which the production of alatae is determined. The data suggest that this occurs shortly after birth.

The material is well organized and readily accessible to the reader. The publication includes a detailed discussion of previous work and a short section dealing with the life cycle of the spotted alfalfa aphid, but the bulk of the text is devoted to the presentation of data and interpretation of the results of the experiments undertaken. There are 14 figures and 12 tables. Drawings of the various developmental stages of the spotted alfalfa aphid are adequate for the author's purpose but deficient in many structural details. The section on the life cycle is somewhat misleading. The spotted alfalfa aphid is stated to have a life cycle that is typical of the Aphididae, but as this species is apparently completely parthenogenetic it can scarcely be considered typical in this respect.

The fact that the species used in the experiments is parthenogenetic may have lent a degree of accuracy to this work that was not obvious in some previous, similar experiments. It must be remembered that most species of aphids during normal development, especially those that have alternate hosts, produce more than one type of agamic alate. Therefore, if this factor is not taken into account, it is conceivable that various induced experimental conditions could trigger the production of more than one type of alate with confusing results. This possible source of error has been virtually eliminated in the present work.

W. R. Richards

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